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Winter Chinook salmon in the Central Valley of California: Life history and management

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ABSTRACT

Winter Chinook is an endangered run of Chinook salmon (*Oncorhynchus tshawytscha*) in the Central Valley of California. Despite considerable efforts to monitor, understand, and manage winter Chinook, there has been relatively little effort at synthesizing the available information specific to this race. In this paper we examine the life history and status of winter Chinook, based on existing information and available data, and examine the influence of various management actions in helping to reverse decades of decline.

Winter Chinook migrate upstream in late winter, mostly at age 3, to spawn in the upper Sacramento River in May – June. Embryos develop through summer, which can expose them to high temperatures. After emerging from the spawning gravel in ~September, the young fish rear throughout the Sacramento River before leaving the San Francisco Estuary as smolts in January-March.

Blocked from access to their historical spawning grounds in high elevations of the Sacramento River and tributaries, winter Chinook now spawn below Keswick Dam in cool tailwaters of Shasta Dam. Their principal environmental challenge is temperature: survival of embryos was poor in years when outflow from Shasta was warm or when the fish spawned below Red Bluff Diversion Dam (RBDD), where river temperature is higher than just below Keswick. Installation of a temperature control device on Shasta Dam has reduced summer temperature in the discharge, and changes in operations of RBDD now allow most winter Chinook access to the upper river for spawning.

The spawning run of winter Chinook declined steadily from the 1970s to the mid-1990s, with particularly sharp declines in 1976 and 1977 attributed to high water temperature. Since the mid-1990s the spawning population has increased at a mean cohort replacement rate of 145%. Alternative estimates of run size vary, but all are correlated with estimates of subsequent numbers of juveniles. The spatial distribution of spawning has shifted upstream since the change in operations at RBDD and the improvement of fish ladders at the Anderson-Cottonwood dam in Redding. Spawning success has been high in recent years, although gravel limitation may be causing some density-dependent mortality.

Most young winter Chinook leave the spawning reach shortly after emergence, moving down-river gradually to reach the Delta in ~November-December. Within the Delta winter Chinook are difficult to distinguish from other races, and genetic testing has shown that size criteria used to identify winter Chinook are unreliable. Tagged hatchery smolts move down the river and through the Delta rapidly, and about 2.8% survive from release to the Delta. About 3.5% (median) of these fish were estimated to have been killed by the export pumping plants in the south Delta. Winter Chinook leave the estuary in ~February-March at about 100-150mm length. Changes in fishing regulations have reduced harvest mortality to ~20%.

Of the various management actions to protect winter Chinook, the most effective at reversing the decline in abundance have been temperature control at Shasta Dam, opening of RBDD gates for most of the year, and harvest control. Hatchery production has contributed a small but significant amount to the population. Other environmental effects, including flow and climate variables, have no detectable effect on the run size.

Although management has proved very effective in reversing the decline in abundance, the future of winter Chinook is clouded by its inherent vulnerability, climate change, and the likelihood of future severe droughts. To manage and anticipate these changes will require a

more comprehensive and sophisticated monitoring and research program.

INTRODUCTION

Four runs of Chinook salmon (*Oncorhynchus tshawytscha*) are found in California's Central Valley, each denoted by the season in which adults leave the ocean to spawn: winter, spring, fall, and late fall. Historically all four runs were likely quite abundant with the fall and spring runs perhaps being the most numerous (Yoshiyama et al. 1998). Since the Gold Rush, human activities including dam building, water diversions, mining, road construction, hatchery releases, and harvest have severely affected the salmon runs.

Alarmed by declines in abundance, the California-Nevada Chapter of the American Fisheries Society in 1985 petitioned the National Marine Fisheries Service (NMFS) to list winter Chinook as threatened under the Endangered Species Act and in 1987 the Sacramento River Preservation Trust petitioned the California Fish and Game Commission to list it under the California Endangered Species Act. Although agencies were initially reluctant to list the species (Williams and Williams 1991), after the spawning population hit a low point in 1989 the Fish and Game Commission listed winter Chinook as endangered, and NMFS listed winter Chinook as threatened, raising its status to endangered in 1994. This made winter Chinook the first listed Pacific salmon stock and the only run in the Central Valley listed as endangered.

The general life history, including timing of migrations and duration of stream residence, may be unique among Chinook races throughout their range (Healey 1994). Winter Chinook abundance declined sharply through the 1970s – 1980s (see Figure 6), and following a series of management actions began to increase after the mid-1990s. Although this turnaround is promising, the future of winter Chinook is far from assured (Lindley et al. 2006). Our goal is to document our understanding of the biology of this fish and to provide a preliminary assessment of the efficacy of various management actions that have been taken or are contemplated.

In this paper we present a quantitative conceptual model of the winter Chinook population, emphasizing current conditions and management. Healey (1991) described the life history of Chinook populations throughout western North America. Williams (in press) provided a more comprehensive discussion of all races of Chinook salmon and steelhead in the Central Valley, and Yoshiyama et al. (1998, 1999, 2000, 2001) examined the history of abundance, exploitation, and management of the various runs. We assume readers are familiar with general life cycles of Chinook salmon, which are described in the above references. A comprehensive summary of environmental and management influences on winter Chinook is available in NMFS (1997). Models of winter Chinook include analyses of population viability (Botsford and Brittnacher 1998, Lindley et al. 2006), a Bayesian population model emphasizing the influence of striped bass predation on winter Chinook (Lindley and Mohr 2003), and a state-space model of juvenile abundance (Newman and Lindley 2006). Bartholow's (2004) model of Sacramento River Chinook includes a module for winter Chinook.

Much of the information written on winter Chinook is in unpublished reports or government documents, which have formed the basis for management of these fish, but can be difficult to obtain. We examine the available written record on the habitat of winter Chinook, and then use available data and reports to illustrate key aspects of its life history. We also analyze the potential contributions of several management actions to the reversal of the decline in winter Chinook; a separate paper (Ligon et al. in prep.) will incorporate these and other aspects of winter Chinook life history into a state-space model.

Winter Chinook is the most distinct from the other Central Valley runs both genetically (Kim et al. 1999, Banks et al. 2000) and in terms of life history (Healey 1994). Partly because of its unique life history, managing and restoring the winter Chinook population presents several challenges. Winter run adults and juveniles co-occur with the other three runs and it is difficult to distinguish various races at any life stage. Life-history characteristics of the runs are variable enough to allow for considerable overlap in size and the timing of migrations among runs, particularly during spring emigration. The large commercial and recreational fisheries focus mainly on the more numerous fall Chinook, but have taken substantial numbers of winter Chinook.

Figure 1 summarizes the life history of these fish, with a geographic reference and an indication of some of the events or locations discussed in this paper.. We focus on attributes particular to this race; see the above references for the general biology of Chinook salmon.

BACKGROUND

Habitat

The extant inland habitat for winter Chinook differs markedly from its state when the run evolved. Historically winter Chinook spawned in cool, spring-fed streams such as the McCloud and Pitt rivers and Hat Creek, in the upper reaches of the Sacramento River system (Slater 1963, Fisher 1994, Yoshiyama et al. 1998, 2001). The cool water and relatively constant flow allowed this race to spawn during the summer, when high temperatures precluded successful spawning of salmon in most Central Valley streams. Since construction of Shasta Dam, winter Chinook spawning has been restricted mainly to cool tailwaters of the Sacramento River between Keswick Dam and the City of Red Bluff (about 50 km downstream, Figure 2) (Yoshiyama et al. 2001, Williams in press), although adult winter Chinook have been observed in Battle and Mill creeks (Hallock and Fisher 1985). There are anecdotal accounts of a historic winter run salmon in the Calaveras River but current conditions are such that the run could not survive (E. Gerstung, CDFG, retired, personal communication). Otherwise winter Chinook are now confined exclusively to the mainstem Sacramento River for spawning and rearing.

We describe the current state of the habitat of winter Chinook with emphasis on conditions that have changed, and that are likely to affect the abundance or distribution of winter Chinook (see NMFS 1997, Good et al. 2005). These conditions include dams, major diversions and other alterations to flow, and contaminant sources. These brief descriptions set the stage for the analysis of life history and response to management.

Dams and Diversions Shasta Dam was completed in 1945 at river kilometer 498 (Figure 2). Shasta Reservoir has a storage capacity of about 5.6 billion cubic meters, making it the largest reservoir in California. Shasta's capacity is nearly equal to mean annual discharge (~7 billion cubic meters from 1988 to 2004). Minimum carryover storage in summer averages 3.3 (range 0.7 – 4.5) billion cubic meters, the lowest minimum occurring during the drought of 1976 – 1977.

The high carryover storage and depth (maximum 158 meters) of Shasta reservoir ensure that the deep cold-water pool remains available in all but severe droughts. However, flow through the hydropower generating plant is taken from a high point in the reservoir. When winter Chinook was listed in 1989, Biological Opinions for winter Chinook (National Oceanic and Atmospheric

Administration, NOAA) and actions by the California State Water Resources Control Board (SWRCB) to protect fish habitat specified that average daily water temperatures at Red Bluff could not exceed 56 °F (13 °C) when such temperatures would adversely affect winter Chinook. The US Bureau of Reclamation (USBR), which operates Shasta Dam and Reservoir, could meet the standard in most years by releasing flow from the hypolimnion, but this water bypassed the hydropower plant, resulting in significant economic loss. In 1997 the USBR completed construction of a temperature control device in Shasta Reservoir to direct cold hypolimnetic water through the hydropower plant (Lieberman et al. 2001), keeping the spawning area cool without forgoing power production.

Keswick Dam, a re-regulation dam for flows from Shasta Reservoir, was completed in 1950 at river kilometer 486. Keswick and Shasta Dams lack fish ladders, so spawning is now confined to the mainstem river below Keswick and in recent years above Red Bluff Diversion Dam (see below). Spawning habitat in this reach may be gravel-limited because Shasta Dam blocks the downstream movement of gravel and the reach through Redding has been extensively mined for sand and gravel, in part to build Shasta Dam (M. Kondolf, UCB, pers. comm.). Gravel has been augmented several times (for example see Bigelow 1996 for evaluations of 9 gravel augmentation projects completed in 1990 and 1991).

The Anderson-Cottonwood Irrigation District (ACID) dam was privately constructed in 1918 in Redding at river kilometer 481. This dam comprises a frame and a series of flashboards that are added or removed to adjust the head. Dam configuration can be changed only at low flow, which often requires adjusting flow from Keswick dam; historically these changes were made rapidly, possibly resulting in disruption of spawning by winter Chinook (NMFS 1997). Fish ladders were constructed to bypass the ACID dam but, because they were found to be ineffective, they were modified in 2001 to improve passage of adult Chinook (discussed below).

The Red Bluff Diversion Dam was completed in 1966 at river kilometer 391 to provide head for diverting water into the Tehama-Colusa Canal. The dam consists of a series of gates that can be lowered into the river to manipulate the river stage upstream. When the gates are all raised out of the water there is no impediment to flow or passage of fish. Fish ladders on both sides of the dam, intended to allow for passage and also allow for counts of the migrating adults, suffered from lower than optimum attraction flows and were not completely effective (USBR 1997, CDFG 1998). When the RBDD gates are lowered, fish are delayed in their migration and may spawn downstream from the dam rather than continuing upstream. Hallock et al. (1982) found a significant correlation between delay time and the proportion of total flow passing in or near the RBDD fishways. Juvenile salmon emigrating when the dam gates are lowered suffer mortality due to predation, mainly by striped bass and pikeminnows (USFWS 1981, Tucker et al. 1998).

Beginning in 1986, the USBR raised the RBDD gates seasonally to protect winter Chinook and other anadromous salmonids. To comply with the 1993 and subsequent NOAA biological opinions for winter Chinook and other listed anadromous salmonids, the gates are now raised from September 15 through at least May 14 of the following year. This schedule permits all but an average of 15% of the adult winter Chinook to move past the dam with little or no delay (see below). The new gate operating schedule also appears to have reduced predation on juvenile Chinook salmon to less than significant levels (Tucker et al., 2003).

Before RBDD gates were raised most of the migrating adult salmon passed through the fish ladders and were counted. Now that the gates are open during most of the winter Chinook

migration, estimates of adult passage must be extrapolated from the ladder counts using the average ratio of total migration to migration during the dams-closed period, based on data from before dam closure. This introduces considerable uncertainty into the passage estimates based on ladder counts (Newman and Lindley 2006).

The Glenn-Colusa Irrigation District (GCID) operates a diversion on an oxbow off the Sacramento River at river kilometer 320 (Figure 2) that can divert up to $85 \text{ m}^3 \text{ s}^{-1}$ (3000 cfs). This diversion was modified in 1992-1993 to improve salmon passage, and rebuilt in 2000 with improved fish screens and bypass flow. Although the GCID diversion was considered a hazard to winter Chinook before redesign (NMFS 1997), most juvenile winter Chinook migrate past GCID in September-October, after the peak irrigation period. Therefore it is unlikely that substantial numbers of winter Chinook were entrained. Screw trap sampling at the diversion provides additional data on the movements of juvenile salmon down the Sacramento River.

The Sacramento-San Joaquin Delta The Delta is a complex network of channels forming the landward limit of the San Francisco Estuary (Figure 2). Most of the time the Delta is a tidal freshwater region (Kimmerer 2004). The Delta provides a migratory pathway for emigrating juvenile salmon and habitat for rearing. The Delta has been the focus of many actions to improve conditions for juvenile Chinook salmon, including winter run, because this region may be hazardous to salmon for two somewhat interrelated reasons: first, because of the possibility that fish are vulnerable to predation and other sources of mortality in the Delta channels; and second, because of export pumping of freshwater from the Delta (Kjelson et al. 1989).

The State Water Project and Central Valley Project operate export pumping facilities in the south Delta (Figure 2) with a combined capacity to divert about $425 \text{ m}^3 \text{ s}^{-1}$ (15,000 cfs) from the Delta, although typically maximum combined pumping rates are capped at around $340 \text{ m}^3 \text{ s}^{-1}$ (12,000 cfs). This pumping has three general effects on the Delta. The first, most obvious effect is the entrainment of fish, many of which are subsequently salvaged in fish facilities associated with the pumping plants (Brown et al. 1995). The second is the alteration of net flow patterns within the Delta, which can affect how juvenile salmon migrate downstream through the Delta. The third is the requirement to release water from reservoirs to allow for pumping in the Delta, so that during summer flow is higher and the water fresher than it would have been before export pumping began. In addition to the major export plants, more than 2000 local agricultural diversions (Herren and Kawasaki 2001) could also have an effect on emigrating juvenile salmon, although this effect has not been quantified and is probably low (Nobriga et al. 2004).

The fish facilities provide important data on the abundance and movements of salmon and other fish, but interpreting these data is difficult. Fish are concentrated continuously by a series of louvers and periodically trucked from the collection tanks to release points in the estuary. Ten-minute or longer samples of fish are taken at 2-hour intervals throughout the day and night. Fish are periodically identified to species and measured, and salmon with clipped adipose fins (which indicate they have been coded wire tagged) are sent to a laboratory to extract and decode the tag. The counts by species and length are extrapolated to estimate the total numbers entrained each day.

The estimates of the numbers of salmon and other fish salvaged provide valuable data on abundance per unit volume. However, mortality due to predation at the intakes to fish facilities can be very high and variable, particularly in Clifton Court Forebay, a regulating reservoir for the SWP (Brown et al. 1996). This predation loss results in uncertainty of up to an order of

magnitude about the number of fish that arrive at the facilities. In addition, length criteria used to distinguish winter Chinook from other stocks in the Sacramento River (see later discussion) are ambiguous in the data from the fish facilities, so the assignment of salmon to race is uncertain. This problem is being addressed through genetic analyses (Banks et al. 2000), but to date the data have not been widely available and the genetic program has not resolved the question of how many winter Chinook are taken (killed directly) at the water project intakes.

The Delta Cross-Channel (DCC), on the Sacramento River near Walnut Grove (river kilometer 41, Figure 2), was constructed in the early 1950s to convey Sacramento River water through the interior Delta to the CVP pumps in the southern Delta. Flow into the DCC is controlled by stage difference between the Sacramento and Mokelumne Rivers and is not affected by water project pumping from the South Delta. The DCC is gated, with the gates normally closed to protect interior Delta channels from scouring when Sacramento River flow exceeds about $700 \text{ m}^3 \text{ s}^{-1}$ (25,000 cfs). As a result of the 1993 and subsequent biological opinions, the DCC gates are now closed each year from February 1 through May 20 to protect emigrating juvenile Chinook salmon. The California Department of Fish and Game (CDFG), U.S. Fish and Wildlife Service (USFWS) and NMFS can also request up to 45 days of gate closure during October 1-January 31 to protect emigrating winter and spring Chinook salmon. The presumed benefits of the gate closures are based on results of mark-recapture studies conducted since the early 1970s (Kjelson and Brandes 1989, Brandes and McClain 2001, Newman 2003).

Temperature Because winter Chinook eggs and alevins develop through summer, high water temperature can limit the amount of habitat where survival is possible. During the drought of 1977, for example, high river temperature probably killed every winter Chinook produced in the river. Even earlier, when Shasta Dam had been completed but not yet filled, winter Chinook went through a period of very low abundance, probably in the hundreds, because of high temperature in the available spawning habitat (Slater 1963). After temperatures were reduced in the dam's tailwaters, winter Chinook reached abundance almost as great as that of fall run (Slater 1963). Because of its importance to management for winter Chinook, temperature is discussed in some detail below.

Contaminants The Superfund site at Iron Mountain Mine is by far the largest source of heavy-metal contamination in the Sacramento watershed (US Geological Survey 1990). Drainage from Iron Mountain Mine into Spring Creek, and then into the Sacramento River, has numerous potential ecological impacts (Saiki et al. 2001) and has been cited as the cause of numerous fish kills (NMFS 1997). A dam on Spring Creek has allowed the USBR to regulate discharge of contaminated water to the Sacramento River since 1980. Treatment facilities installed in 1994 reduced loading of metals into the Sacramento River. Since 1996, several remedial actions have decreased heavy-metal loading from Iron Mountain Mine and in 2004 construction of Slickrock Creek Retention Reservoir reduced contaminants from this source by 95% (U.S. EPA 2006). However, the timing of most of the recorded fish kills attributed to toxins does not match the timing of life history stages of winter run salmon: all of the reported fish affected fry in spring, except for one kill of fry in November 1981, and one kill of an unknown fraction of eggs and fry in June 1986 (NMFS 1997).

Other sources of contamination are unlikely to affect winter Chinook either because the fish are not exposed (e.g., agricultural chemicals applied in spring), or because the exposure is likely to be brief (e.g., selenium in the San Francisco Estuary near Carquinez Strait, Doblin et al. 2006)

Hatcheries Since 1989 winter Chinook have been propagated at the Coleman and Livingston Stone national fish hatcheries (except in 1996 and 1997) and in small captive broodstock populations maintained at the Steinhardt Aquarium in San Francisco and at the Bodega Marine Laboratory (Table 1). Artificial propagation serves to supplement the population and speed recovery, and the captive broodstock program was insurance against potential catastrophes in the natural environment that could decimate a year class. Initial efforts to propagate winter Chinook at Coleman National Fish Hatchery (CNFH) on Battle Creek led to problems with imprinting of fish on Battle Creek water and to hybridization with spring Chinook (NMFS 1997), so the program was moved to the Livingston Stone National Fish Hatchery (LSNFH).

The LSNFH was built at the base of Shasta Dam in 1997, and propagation of winter Chinook at CNFH was discontinued. Adult salmon for the propagation program are collected at a fish trap at Keswick Dam, and their identity as winter Chinook is verified by genetic testing. All of the fish produced at LSNFH are tagged with coded wire tags (CWTs) and the adipose fin is clipped. All production is released as advanced smolts in the Sacramento River near Redding, typically in January. Since winter Chinook produced at LSNFH imprint on Sacramento River water in the hatchery, the assumption is that the hatchery and naturally spawning population comprise a single population. This assumption is supported by data from the spawning ground showing that hatchery returns and naturally spawning fish spawn at the same age, same time and same location (Niemela as cited in Brown and Kimmerer 2004). The winter Chinook Evolutionarily Significant Unit (ESU) includes the naturally spawning population, the LSNFH population, and small captive broodstock populations maintained at the LSNFH and Bodega Bay Marine Laboratory (NOAA Fisheries, 2005).

Because the LSNFH is a supplementation hatchery, hatchery protocol has been developed and applied to ensure that hatchery operation does not compromise the genetic integrity of the wild winter run (Hedrick et al. 2000). For example, no more than 15 % of the wild run can be taken into the hatchery (maximum of 120 fish) for spawning and no more than 10% of the hatchery broodstock consists of hatchery returns (USFWS 2001). In 1996 and 1997, when neither Coleman nor Livingston Stone were operating, the captive broodstock program being operated under the auspices of the University of California (Davis) Bodega Marine Laboratory provided small numbers of smolts for release (Hedrick et al. 2000, Arkush et al 2002).

Life History

The life history of winter Chinook (Figure 2) is generally similar to that of other Central Valley Chinook except for the timing of events, particularly the incubation of embryos through summer. Here we introduce some of the key features which are explored in detail below. Winter Chinook adults enter the Sacramento River as “green” fish, not fully mature (Slater 1963), mainly at age 3 but with some at ages 2 and 4. The peak of migration past RBDD (the first opportunity to observe the migration) occurs in March – April (Yoshiyama et al. 1989). Spawning occurs in the mainstem Sacramento River, mostly above RBDD and recently above ACID, centered around mid-June. Eggs and alevins develop in the gravel through summer to emerge from July through October (Yoshiyama et al. 1989). Most juveniles leave the spawning reach shortly after hatching in September-October (Gaines and Poytress 2003), although a few rear in the upper Sacramento River. Otherwise juveniles rear throughout the river and the Sacramento-San Joaquin Delta, entering the ocean in December-February.

Since construction of Shasta Dam, key environmental influences on winter Chinook have included blocked access to spawning grounds, high summer water temperature, mortality during downstream migration, and fishing mortality. Management actions to minimize all of these effects are discussed in detail below.

Winter Chinook is the most genetically distinct of the Central Valley runs (Kim et al. 1999, Banks et al. 2000), and hybridization with other runs has apparently not occurred except for a brief period of limited hybridization with spring run in at the CNFH (Banks et al. 2000). Winter Chinook may have gone through a population bottleneck, possibly during the recent decline in abundance (Banks et al. 2000). Concerns about the genetic effects of hatchery propagation include a possible reduction in resistance to pathogens in a population with reduced genetic variability (Arkush et al. 2002) and domestication selection (USFWS 2001). Effective population size of winter Chinook has apparently not been greatly affected by the supplementation program in effect (Hedrick et al. 2000 a).

Adaptation to conditions below Keswick Dam may imply evolution to accommodate the current conditions. Salmon stocks are capable of very rapid evolution of life-history traits (Hendry et al. 2000, Heath et al. 2003), in addition to their well-known phenotypic plasticity.

DATA SOURCES AND METHODS

Data used in this paper were obtained from published papers and reports, publicly available databases (Table 2), or agency personnel. Pipal (2005) summarized monitoring activities in the Central Valley for ESA-listed salmonids. All of the data appear in some form in agency reports and in a handful of published papers. Where possible we obtained either raw data or data aggregated over relatively short time periods. Data include harvest, estimates of the size of the spawning run, and various estimates of juvenile abundance (Table 2). Ancillary data included freshwater flow into (Inflow) and out of (Outflow) the Sacramento-San Joaquin Delta, export flows at the state and federal water export facilities in the south Delta, and river temperature at various stations.

Abundance of adult migrants has been estimated by daily visual counts of fish passing fish ladders at RBDD. Methods are described in detail in an unpublished report (Killam and Harvey-Arrison, 2002); here we describe some features that are essential to understanding the estimates and their variability. Since 1986 changes in dam operations (discussed above) limited the duration of the fish ladder counts to an average of about 15% of the run, so agency biologists have extrapolated ladder counts to account for the time not sampled. In 1995, CDFG and USFWS began conducting carcass surveys to obtain an alternative estimate of numbers of winter run spawners (Killam 2003).

In general all salmon ascending the ladders were counted during the day (14 hours), and twice-weekly counts were made at night to determine a correction to daytime counts, which averaged 1.11 during 1986 - 2004. Sometimes additional adjustments were necessary because salmon could not be observed, such as during high-flow periods or when ladders were being maintained. A trap at the ladder on the east bank was used to capture samples of fish which were identified to run based on phenotypic characteristics such as color (brightness) and apparent degree of gonadal maturity. Counts were summed by week, and the proportion of winter Chinook adults in the trap counts were used to estimate the number of winter Chinook passing the dam each week.

Data for 1967 - 1984 comprise the weekly estimates; apparently the raw data and intermediate calculations are no longer available. Data from 1985 on include weekly ladder counts, trap counts, and adjustment factors so that the entire calculation can be reconstructed.

There are two principal sources of error in the RBDD ladder counts. Error arises from the use of a sample to determine the run of each fish seen in the ladders. In years since 1986, ladder counts have been further extrapolated based on the time period when the gates are down and fish use the ladders, and the proportion of the winter run that passed the dam in that period during 1982 - 1986. Those years were chosen because the run size resembled those in later years (Killam and Harvey-Arrison, 2002). A few other potential sources of error (e.g., from the correction for night counts) are likely to be small and we have ignored them. We assume identification of fish from the traps is correct.

We estimated sampling error in the traps for each week assuming a binomial distribution, and propagated the error into the total counts for the year:

$$\begin{aligned}\hat{N}_W &= N_L p_{TW}, \\ \sigma_{N_W}^2 &= N_L^2 p_{TW} (1 - p_{TW}) N_T\end{aligned}\tag{1}$$

where N_W is the estimate of weekly winter Chinook counts, N_L is the adjusted ladder count, N_T is the trap count, p_{TW} is the proportion of the trap count that was adult winter Chinook, and $\sigma_{N_W}^2$ is the variance of the estimate. The chief assumption here is that the ladder counts N_L are made without substantial error. These equations were used to determine a coefficient of variation, the average of which was applied to years before 1985. This may result in overestimates of the confidence limits, since with larger runs the trap counts were presumably higher and the relative error may have been smaller.

For years after 1986, we determined the mean and variance of the factor used to extrapolate from the limited sampling period. The timing of the run varied considerably (Figure 3), so we used a trimmed mean to determine the statistics, trimming the 2 most extreme values (leaving 15 values). The extrapolation factor was still distributed asymmetrically, so the error due to this factor was determined through simulation. For each year starting in 1987, the week in which sampling began was determined, and the factor corresponding to that week (i.e., the ratio of the total duration of the run to the time sampled) was sub-sampled 100,000 times. This factor was multiplied by a normally-distributed random variable with a mean equal to the estimated adult abundance during the sampled period (the sum of the N_W values) and a standard deviation calculated as the square root of the variance $\sigma_{N_W}^2$. The mean of this product was used as the estimate of adult abundance with upper and lower 90% confidence limits determined as the 5th and 95th percentiles of the product.

Data on the timing of spawning was determined from the date of the mid-point of the counts in the redd surveys, and in the carcass surveys with 2 weeks subtracted to account for the time between spawning and recapture of carcasses (D. Killam, CDFG, pers. comm.). Timing of emergence was estimated by projecting forward from spawning dates to the dates of emergence using a development rate model, or from the peak in catch at RBDD, assuming that most juveniles leave their natal reach upon emergence. Emergence time was calculated from temperature using a Bělehrádek function following the recommendations of Beacham and

Murray (1990). The function, with parameters $a = 0.000030$, $b = 2.04$, and $c = 7.6$, was applied using daily temperature (see below) to calculate fractional development time, which was accumulated for each year from the mid-time of spawning until development was complete.

Abundance of juvenile emigrants at various points on the river has been estimated by rotary screw traps (RST), trawls, and beach seine surveys. Only the RST survey at RBDD has been designed to provide an estimate of absolute abundance, and only this estimate is provided with information about uncertainty. Gaines and Poytress (2003) compared their juvenile production estimates from the RBDD screw traps to both fish ladder data and carcass survey data and concluded that the adult estimates from the ladder underestimated the number of spawners, compared to carcass data. Other RST data consist of catch per day by length, which we averaged by week, except that the data from Knights Landing were provided as catch per week. Examination of effort data indicated that effort was fairly consistent within seasons, so we did not explicitly adjust for effort. Trawl data were converted to mean catch per trawl, and beach seine data to mean catch per seine haul.

Beach seine data were further subdivided by station. Most of the catch of winter Chinook in the beach seine samples was from stations in or near the Sacramento River. We therefore used only those stations in our analysis. In addition, in most years sampling was concentrated in January - June, and only in 2 years was there substantial sampling late in November and December when substantial numbers of winter Chinook migrated downstream. Therefore the beach seine data were used to indicate timing of the run only in those years.

Temperature: Data from 16 stations on the Sacramento River were obtained from the US Geological Survey and California Department of Water Resources. Availability of data since 1987 was moderately consistent, but from 1970-1987 data were generally available from only a handful of stations. We therefore reconstructed daily mean temperature data for 1970 - 2001 as follows. First, for those stations that reported only maximum and minimum daily temperatures, we took the mid-point which is close to the mean daily temperature. Second, nearly all temperature records had a few anomalously high or low values, most of which occurred immediately before or after gaps in the record, suggesting instrument malfunction. We removed data where analysis revealed a change in temperature from one day to the next of more than 2.5 °C that was not reflected in data from other stations, but generally we were conservative in leaving data in the record unless there was clearly a problem. Third, all records had gaps ranging from a day to years. We filled in gaps of a week or less by linear interpolation. The next step was to fit a seasonal cubic spline to the data from each station to represent the long-term average seasonal pattern for that station. The spline was fit with 12 internal "knots", or points of inflection, to capture most of the seasonal pattern irrespective of shape. We omitted the last day in all leap years from this analysis to keep the days and seasons aligned.

The residuals, i.e., the repaired data minus the seasonal spline (using values from day 365 for day 366 of leap years), were then analyzed for spatial and temporal patterns. Two patterns emerged: variance decreased with distance upstream, and residuals were strongly autocorrelated in space (i.e., among stations) and time. We calculated residual temperature values for each station and day as follows. First we divided all data from each station by the inter-quartile range of residuals from that station to scale the data similarly. Next we calculated median residuals for all non-missing data for each day, and multiplied those values by the inter-quartile weighting factor for each station. This put all values back into the original scale. Finally, we added the residuals to the spline predictions to arrive at predicted temperature values for each day and station. Residual

standard errors based on regressions of predicted vs. observed values for each station were around 1 °C, decreasing from downstream to upstream as the temperature range decreased (Table 3). Predictions for each station being compared were calculated without that station, although all available stations were used in the final calculation of temperature, so these standard errors are conservative. The final data matrix comprised all available measured data (with anomalous values removed as described above) with gaps filled in with the reconstructed data. Data after 2001 were included simply as daily values from the temperature records, with short gaps filled by interpolation as described above.

As an alternative we also used output from a model of temperature in the Sacramento River (Deas et al. 1997). This model provides a reconstruction of temperature in the upper 72 km of the river for 1970 – 2001.

Sacramento-San Joaquin Delta: The export facilities in the south Sacramento-San Joaquin Delta may pose a threat to the survival of juvenile Chinook salmon during migration through the Delta. (Kjelson and Brandes 1989) We used the previously described salvage calculations to estimate numbers of winter Chinook based on size criteria, and also to estimate the number of winter Chinook marked with coded-wire tags and released by LSNFH that were subsequently recaptured at the fish facilities.

We likewise calculated the flux of winter Chinook (by size) and marked winter Chinook recaptured in the Chipps Island trawl and used these to estimate the flux of fish migrating past Chipps Island at the western edge of the Delta. This flux is the number of fish per unit volume times the rate of seaward movement of the fish. We determined the number of fish per volume from the net area and the distance towed from the flow meter reading on the net (Brandes and McLain 2001), with the grand mean used to fill in for missing values. The rate of movement of fish was determined from the rate at which coded-wire-tagged fish from LSNFH moved between Sacramento and Chipps Island, which we estimated at about 16 km d⁻¹. Fish were assumed to migrate only in the top 4m of the water column (Brandes and McLain 2001). Note that our method differs from that used by Brandes and McLain (2001) in that we use the estimated speed of the fish to calculate flux past Chipps Island.

Tagged fish were recovered over variable time spans, and there were often a few stragglers that were not recovered for several months. We therefore estimated the fish flux for the time from the first recovery until ~99% of the fish had passed as determined from all recapture data. The fraction of salmon lost at the fish facilities was calculated as the difference between the fish flux going to the facilities and successful salvage. The fish flux was the extrapolated capture rate divided by the louver efficiency and the fraction not lost to pre-screen mortality; calculations are presented in detail in Brown et al. (in prep.).

Tissue samples have been taken from Chinook collected in the lower Sacramento River and the Delta, particularly at the fish facilities, to identify fish to run based on genetic methods. We are unaware of any metadata or written sampling protocol, and the samples do not appear to have been taken in a stratified random sampling program. Winter Chinook is the most distinct run (Banks et al. 2000) with a low rate of false positive identifications. However, in a mixed stock analysis including a rare and a common species or race, even a low rate of false positives can result in a substantial total number of incorrect identifications (Hedgecock 2002). Hedgecock (2002) reported provisional identification of the Chinook salmon sampled in this program to winter run or to other runs based on 5 microsatellite loci or in some cases 7 loci.

Because this identification is provisional pending peer review of the methods (Banks and Hedgecock in prep.), we use only the overall patterns and apply no statistical tests to the results. Chinook collected in the genetic program were assigned to winter run (N=1030) or other runs (N=8001), although about 10% of the fish could not be assigned. A total of 6752 identifiable Chinook were taken from the fish facilities, and 85 from the Knights Landing screw traps, 1516 from the Sacramento River trawl, and 682 from beach seine sites in the Delta. We focused on the larger data set from the fish facilities.

Management actions: We developed a simple model to investigate the effectiveness of the various management actions undertaken in the last ~15 years (Table 4). The model is captured by the following equation:

$$N_{\varphi 3} = (N_{\varphi 0} F S_1 + H) S_2 S_3 S_4 S_5 \dots \quad (2)$$

Where $N_{\varphi 3}$ is the number of females at age 3 years, $N_{\varphi 0}$ is the number of females in the previous generation (3 years earlier), F is fecundity, H is hatchery input, and the S values are survivals over various life stages or events. Model assumptions are:

- Density dependence is minimal
- All females return to the river at age 3
- Sex ratios and fecundity are constant among years
- Survival from egg to juvenile (S_1) is constant as long as there are no thermal or toxicity-related mortality events.
- Hatchery inputs occur at the same life stage every year, which is equivalent to juveniles passing RBDD.
- Redd distributions in years without surveys were the same as the average of years with surveys and similar operation of the RBDD gates.

Under the first assumption the S values are independent of each other and of population size. The S values were estimated as described below, except for a single free parameter representing survival over times when estimates were not available, i.e., most of the life cycle. We used available data to estimate the numeric effects of actions whose effects on the salmon could be quantified (Table 4), calculating cohort replacement rates (CRR) for each brood year. We then applied linear regression analysis to determine whether residual variance (i.e., the difference between CRR from the data and that from the model based on effects of quantifiable actions) could be explained by other variables including management actions. In all cases assumptions of the linear model were tested using graphical analysis of the predictors, response, and residuals.

The effects of RBDD on adult passage were examined by Hallock et al. (1982) who radio-tagged adult fish below the dam and then observed the time needed for them to pass the dam. Passage times were often long (1-40 days) and slightly negatively related to flow. In addition, CDFG conducted aerial redd counts in 1982, 1985, and every year since 1987. We used the redd counts to determine the proportional distribution of redds by river reach for each year in which redds were surveyed, and used the mean distribution from 1982-1988 for earlier years. The Hallock et al. (1982) relationships did not help to explain the distribution of redds, because flow explained only a small proportion of the variance and there was a lot of uncertainty about the effect of

duration of delay on the spawning distribution and success, particularly for winter Chinook which do not spawn immediately on reaching their spawning grounds.

Effects of opening RBDD gates during downstream passage have not been measured. Gates were opened at the end of each year (after the winter-run emigration season), then on 30 October 1992, 15 October 1993, and the middle of September since then. This falls about in the middle of the emigration period for the majority of winter Chinook (Gaines and Poytress 2003). Pre-smolts and smolts emigrating later would have encountered closed gates before 1992.

Temperature in the model affected development time and thermal mortality to the eggs and alevins, since the peak temperatures occur during summer when eggs are incubating. Two problems confronted this analysis: gaps in the temperature data as discussed above, and the lack of a tested functional relationship among temperature, duration of exposure, and mortality. Reports on the temperature tolerance of salmon eggs and alevins usually provide a range of temperature with no reference to time of exposure. Translating this into an actual survival function based on realistically-varying temperature data is not simple. Myrick and Cech (2004) summarized thermal effects on Chinook salmon, including effects on eggs and alevins. Their Figure 1 shows reduced survival at $\sim 14\text{--}15^\circ\text{C}$ and no survival at temperatures above $\sim 18^\circ\text{C}$. These results were based on several studies with an unspecified duration of exposure. Bartholow (2004) constructed a simulation model of juvenile Chinook production in the Sacramento River using a weekly thermal mortality for eggs and embryos that increased sharply from ~ 0.1 at 15°C to ~ 0.9 at 17°C .

The only experimental analysis of thermal effects on winter run Chinook eggs and alevins is that done by USFWS (1999), which also reported experiments on fall-run. We adapted the data from this study to develop a thermal mortality model. Eggs and alevins were incubated at several nominal constant temperatures ($13.3\text{--}17.8^\circ\text{C}$ for winter-run, and $10\text{--}16.7^\circ\text{C}$ for fall-run), and with several increases from nominally 13.3°C to either 15.5°C or 16.7°C at about 0.5°C per day. Temperatures were recorded and plotted but actual temperatures fluctuated and statistics were not reported; we took the nominal temperatures as the actual temperatures. Eggs were taken from 3 (winter run) or 5 (fall run) females and divided among treatments for replication. Data reported were number of eggs at the beginning of the experiment, eggs that were not viable, and the number remaining at various life stages identified by accumulation of temperature units. We combined data for various egg stages to obtain survival from spawning to hatching.

We calculated daily mortality rates from the above data for both fall-run and winter-run Chinook, assuming that reported deaths during various intervals represented a constant mortality rate during egg development and during alevin development. These mortality rates were then plotted against temperature during the incubation using either the nominal temperature or the time-weighted mean based on the two nominal temperatures. The results suggested a log relationship above about 13.3°C and a constant mortality rate at lower temperatures. The data from 13.3°C and higher fit a log-linear relationship, which for eggs did not differ between the winter and fall Chinook (Figure 4A), although differences among the progeny of different females were noted.

The fit for alevins was complicated by several factors. First, the alevins were transferred to larger containers in aggregate before they reached the end of the life stage at lower temperatures. Therefore the duration of this part of the experiment was brief and uncertain. Second, high residual mortality at low temperature (Figure 4B) made the temperature effect difficult to

distinguish from the residual mortality. We therefore subtracted the mean mortality for all data with nominal temperature below 13.3 °C from the remaining data, and fit linear regressions only to those data. This analysis gave a steeper slope for both eggs and alevins, and higher mortality for alevins than for eggs, as has been reported (e.g., Myrick and Cech 2004). We used these analyses to provide daily mortality rates, which were as follows:

$$m_{\text{egg}} = e^{-20.62 + 1.01 T} \quad (3)$$

$$m_{\text{alevin}} = e^{-18.12 + 0.96 T} \quad (4)$$

Error estimates are not presented here because they would be misleading given the few families of fish actually investigated and the likelihood that some of our assumptions were wrong. This analysis was used to set up a hypothetical model of mortality, which we checked by examining the relationship of residuals with temperature (below). We also applied an alternative approach which was to assume that temperature above 16°C resulted in complete mortality.

We used the daily temperature data for each sampling point to calculate survival during each year from the assumed spawning date (taken to be Julian day 170, usually 19 June) to the calculated mean emergence date (Julian day 260, or 17 September). Then we calculated a total survival weighted by the spawning distributions. We had no information on the survival of swim-up fry specific to winter-run Chinook, although generally this life stage is less sensitive to high temperature than are alevins (Myrick and Cech 2004, Bartholow 2004). The temperature data indicate that near Keswick Dam the temperature remains at about the same level, even warming somewhat, well into fall in some years. Temperature further downstream decreases more rapidly but from a higher summer value; thus there does not seem to be much thermal refuge for emerging fry in the fall. Nevertheless we were reluctant to extrapolate any further than we already had, so we ignored thermal mortality to swim-up fry.

The first few terms in Equation 2 include several quantities that have been estimated but are not measured routinely. However, the Juvenile Production Index (JPI), an estimate of the number of winter-run salmon passing RBDD, has been determined for 7 years starting in 1995, a time period when thermal mortality was negligible (see Results). The JPI is strongly correlated with adult escapement based on RBDD ladder counts, but much better correlated when data from carcass surveys are used (Gaines and Poytress 2004). Using the RBDD ladder counts for total adults (because the data set is more complete), we calculated a regression with zero intercept, which had a slope of 1135 ± 318 (95% CL) fry equivalents per adult; the mean ratio of fry equivalents to adults weighted by the number of adults was 1329 ± 600 . We therefore applied a fixed ratio of 1200 surviving fry per adult, applying thermal mortality after making this calculation.

The effect of hatchery production was determined by simply adding the hatchery output to the total juvenile production at RBDD as shown in Equation 2. Hatchery production from three sources was obtained from various reports (Table 1).

Ocean harvest of all Central Valley Chinook salmon is determined annually by the Pacific Fisheries Management Council. The harvest is not broken down by run, so PFMC calculated a Central Valley harvest fraction, equal to catch/(catch + escapement), for all Central Valley

stocks. We assumed that the interannual changes in fishing mortality were similar for winter-run and total Central Valley stocks (see below), all the fishing occurs 6 months before migration, and annual natural mortality is 20%; results are not very sensitive to the magnitude of natural mortality. Harvest mortality was estimated from harvest fraction as follows:

$$H = \frac{C}{C + E} = \frac{fN}{N(1 - f)e^{-mt}} \quad (5)$$

where H is harvest fraction, C is catch, E escapement, f is fishing mortality, N is the number of fish in the population, m is the natural mortality rate assumed to be 20% y^{-1} , and t the time period between the harvest and escapement. Setting survival $S = e^{-mt}$ and rearranging gives:

$$f = \frac{SH}{1 + SH - H} \quad (6)$$

A winter run harvest index was determined using marked fish by Hallock and Fisher (1985) for brood years 1969 and 1970, and by CDFG for brood year 1991, although few fish were recaptured from that brood year. Grover et al. (2004) reported cohort reconstruction for brood years 1998-2000 including calculated "impact rates" defined as total mortality due to the fishery including mortality to fish not landed. The mean ratio of impact to fishing mortality in the latter 3 years was used to estimate impact of the first 3 years of winter-run harvest data. A regression between the 6 values of impact and corresponding total Central Valley fishing mortality, calculated as described above, was used to fill in the time series of winter-run fishery impacts.

The result of the above calculations was a time series of synthetic cohort replacement rates (CRR). A single survival term was inserted (the free parameter described above) to make the mean CRR match that of the data, i.e., to make the ratio of final and initial escapement the same. This model output was then compared to measured CRR values, and residuals (measured - modeled) were used in graphical and regression analyses on several environmental variables to determine if any of them was likely to have played a substantial role in the recovery of winter-run salmon. Environmental variables included in the analysis are listed in Table 5 along with sources of data. Each variable was averaged over a time period suitable for its effect on the population. The two indices of ocean condition were averaged over January-June during the period when the winter-run salmon were entering the ocean. Robust regressions (rlm, Venables and Ripley 2002) were used because there were several apparent outliers in the data; robust regression is resistant to extreme values.

RESULTS AND DISCUSSION

Stream Temperature

The reconstructed stream temperatures show the expected seasonal and spatial patterns as well as substantial interannual variability (Figure 5). Reconstructed summer temperature exceeded 16°C in water coming out of Keswick reservoir during 1977 and for a brief period in 1976. Peak temperatures after the advent of temperature control were lower, even during drought years. The cold-water pool in Shasta Reservoir has not been exhausted since 1997.

Spawning Migration and Population Size

Winter Chinook mature mostly at age 3, with a variable percentage returning to freshwater at age 2. Very few return at age 4. For 1971 through 1975 the returning population averaged 25% age 2 years, 67% age 3, and 8% age 4 (Hallock and Fisher 1985). Fisher (1994) using more years of data, gave these proportions as 1% age 2, 91% age 3, and 8% age 4. However, during 1986 - 2003 the fraction of age-2 fish in the adult count at RBDD was estimated to average 32% (range 2 - 75%). Hatchery-reared males were more likely to return at age 2 than naturally spawning fish (Niemela as cited in Brown and Kimmerer 2004). USFWS (2001) reported an average sex ratio of 0.7:1 (M:F; range 0.7:1 to 1.4:1) during 1998 - 2000 for genetically confirmed winter Chinook spawners captured at the Coleman National Fish Hatchery (CNFH) fish barrier weir. Winter Chinook females collected at the CNFH between 1956 and 1982 had an average fecundity of 3,353 eggs per female ($N = 234$, Hallock and Fisher 1985), although more recent studies at LSNFH gave estimates of 4,923 eggs per female. The difference could be due to differences in age and therefore size of the females.

The first point at which winter Chinook abundance can be assessed is during migration past the RBDD ladders. Confidence limits around estimates of the number of winter Chinook passing RBDD have increased because of the need to extrapolate ladder counts to the entire migration period (Figure 6). These confidence limits always include the CDFG estimates although the estimates tend to be below the extrapolated value.

The trend in the spawning population of adults, as inferred by a broken-line fit to the extrapolated ladder data, showed a decrease at an overall cohort replacement rate of 76% from 1967 until 1993, followed by an increase at an overall cohort replacement rate of 145% (Figure 6). The use of this fit implies that all fish return to the river and reproduce at age 3, which is not the case (see above). However, including variable numbers of fish at other ages introduces considerable uncertainty without adding much resolution (Newman and Lindley 2006). The extremely low value in 1980 reflects poor survival of offspring from the 1977 brood year due to high temperature in the tailwaters of Shasta Dam (Figure 5).

Variability around the lines in Figure 6 is substantial, because of temperature effects discussed above, and demographic and sampling variability at low population size, but also because it is unlikely that a constant cohort replacement rate applied throughout each of these periods. Nevertheless, there was no evidence of curvature in these lines, and no autocorrelation in the residuals, suggesting that the broken line captured most of the variability over time scales longer than a single generation.

The various estimates of adult abundance are not completely in accord, although all three indicate a similar recent trend (Figure 6). The revised estimates based on ladder counts were generally somewhat higher than those previously reported. The carcass surveys usually estimated more fish than did the ladder counts in the same years. Although carcass counts also

have biases, particularly in small and heterogeneous streams, it seems unlikely that carcass counts overestimate the population. Beginning in 2001 the carcass surveys have been used to provide official estimates of spawning stock size, partly because of the need to extrapolate from the ladder counts at RBDD, but also because carcass counts gave results more consistent with subsequent estimates of juvenile migration at RBDD (Gaines and Poytress 2003).

Spawning and Development

Hallock and Fisher (1985) showed that spawning may occur from mid-April through mid-August, with most fish spawning in May and June. Niemela (cited in Brown and Kimmerer 2004) showed a somewhat later temporal distribution of spawners (peak in late June/early July) indicating some annual variation in timing of spawning. Redd surveys gave a range for median spawning date between 7 May and 2 July, whereas carcass surveys gave a range from 9 June to 25 June for about half the years sampled in the redd survey.

The median date of adult passage by RBDD varied by over 2 months during years when gates were in place (Figure 3), not including 1979 or 1980 when there were very few fish. In addition, the midpoint of spawning, as inferred from redd surveys, varied by as much as two months. There was no apparent relationship between the median dates of passage at RBDD or spawning and environmental variables, including flow and temperature.

Spawning occurs at water depths up to ~5m (NMFS 1997) and most of the redds are constructed close to shore (F. Ligon, pers. comm.). The large-scale spatial distribution of spawning was determined by aerial redd surveys conducted in most years since 1982 (Figure 7). Before the RBDD gates were open for the full period in ~1990, a substantial proportion of the fish spawned below RBDD. No relationship could be found between this proportion and flow in the river. Among the fish that spawned above RBDD before 2001, ~75% spawned between ACID and the Airport Road bridge 23 km downstream near Anderson, and ~35% spawned in the 3 km immediately below ACID. After ACID fish ladders were upgraded, 47% of the redds were found above ACID and 98% in the upper 30 km of the available habitat, leaving 65 km virtually unoccupied. This distribution of spawning is consistent with observations at other terminal dams, and presumably arises because the salmon evolved to go much further up the river.

Thermal mortality High temperature and a spawning distribution with many redds downstream of RBDD reduced survival during many of the earlier years in the record (Figure 8). In particular, survival by all of our measures was zero in 1977, and either zero or very low in 1976. Other years had periods of high temperature resulting in poor survival by at least some measures. Thermal mortality was reduced first when the RBDD gates were held open beginning in 1986, which moved most of the spawning far upstream (Figure 7). The second reduction occurred with temperature control at Shasta Reservoir, which kept summer temperature in the tailwaters low after 1993 (Figure 5). A third, smaller reduction may have occurred when the area above ACID became more available for spawning, although since that time temperatures have generally not been high enough to have caused significant mortality anywhere above Bend Bridge (Figure 5). Thermal mortality may not be a concern for winter Chinook after emergence, since river temperature is beginning to decline and fry and smolts appear less sensitive to high temperatures than eggs and alevins (Marine and Cech 2004).

Density dependence Relatively little spawning habitat is available in the upper Sacramento River and, as discussed below, most of the fish spawn in a relatively short reach of the river. The stock-recruit data indicate density dependence, but at different carrying capacities in different time periods. Data for brood years 1967 – 1978 show very clear evidence of a statistically significant limit on spawning population size of ~ 30,000 adults (Figure 9A). This limit is highly significant if brood years 1976 and 1977 are omitted, which is appropriate since survival in those years was poor to nonexistent so data from those years is not useful for establishing carrying capacity. From 1982, after the population fluctuations in brood years 1976-1977 had settled down, to 1998 when habitat above ACID became more accessible, evidence for density dependence was weaker with a ~10-fold lower carrying capacity (Figure 9B). This implies a substantial loss of spawning habitat sometime between 1978 and 1982, perhaps due to loss of usable spawning gravel (F. Ligon, pers. comm.). Including hatchery production does not change these conclusions. The data for brood years 1998 - 2002, after substantial spawning began above ACID (Figure 7), are highly variable and do not yet show a clear pattern. Nevertheless, Newman and Lindley (2006) found evidence of density dependence for brood years 1992 – 2001 using a state space model, which (among other refinements) accounts for autocorrelation in the time series. Note that autocorrelation in the residuals from the curves in Figure 9 was negligible.

Emergence and Migration

Median dates of emergence were between 3 August and 24 September for spawning dates from the redd surveys, and 5 and 19 September for the carcass surveys. The narrow spread of incubation time reflects the narrow range of summer temperature on the spawning grounds during these years. Based on a mid-June spawning date and temperature at Keswick Dam (Figure 5), emergence time in the longer record would have ranged from mid-August to the end of September. This is an underestimate of the range of emergence dates since the spawning dates ranged over at least 6 weeks.

During 6 years when both emergence data (based on carcass counts) and RBDD juvenile count data were available, the mode of downstream passage at RBDD occurred within 1 week of the emergence date except for a delay of 3 weeks in 1998, when an earlier, smaller mode occurred 1 week before the emergence date. Thus, for this sequence of years the timing of events in the life cycle of winter Chinook was fairly predictable. These data also show that most of the fish leave the spawning grounds shortly after emerging.

Data on juvenile abundance support the generally increasing trend in adult abundance (Figure 10). Gaines and Poytress (2003) reported a very strong correlation ($r = 0.99$, $N = 6$) between their Juvenile Production Index based on RBDD trap counts and the Juvenile Production Estimate (USBR 2004) based on fecundity, assumed survival of embryos, and adult abundance from carcass surveys. They further reported that the JPE based on ladder counts was less well correlated with the JPI, and consistently underestimated juvenile production compared to the JPI.

Downstream migration

Several sampling points on the Sacramento River and in the Delta can be used to track winter Chinook, although to decreasing levels of reliability moving downstream. Only the RBDD rotary screw trap sampling has been designed and is operated to provide estimates of the total number of fish moving downstream; all others provide some measure of relative abundance.

The winter Chinook were apparently distinguishable in samples within the Sacramento River as a pseudo-cohort based on the size criteria proposed by Fisher (1992). Examples show that the trap sampling at RBDD and GCID, beach seining along the Sacramento River, and the Sacramento trawl all showed peaks in abundance within the size criteria, with lows near the boundaries between criteria (Figure 11). The size criteria appear less reliable for fish larger than ~80mm or for dates later than ~350 days into the brood year, when relatively small groups of fish appear to cross size criteria. We suspect that this is at least partly due to the shape of the size criteria, which assume a constant growth rate even as temperature in the river is declining. For the bulk of the fish the separation of races is clear enough to give confidence that the abundance and timing of the winter Chinook can be determined from these data. These are not true cohorts since fish that pass a sampling site are no longer vulnerable to that site (the beach seine sites and salvage facilities are possible exceptions). This and the protracted emergence period preclude estimates of growth rate for winter Chinook using these data.

Chinook salmon commonly show a downstream movement pattern consisting of an initial pulse of a large number of recently-emerged fry, followed by a long period of migration by larger fish (Healey 1991). This pattern may be due to variability in individual behavior (Bradford and Taylor 1997). Martin et al (2001) described juvenile winter Chinook emigration patterns at RBDD as fitting this pattern but with episodic outmigration periods following high flow and turbidity events. The RBDD data show this initial pulse (examples in Figure 12) and the subsequent movement of larger juveniles. We found little apparent effect of flow on the movement of juveniles based on these data. We did not examine effects of turbidity, which generally increases with flow.

The proportion of fish that moves past RBDD at sizes larger than 60 mm is highest at low abundance (Figure 13). The intercept of the line linking abundance of the two size classes is significantly greater than zero ($p < 0.05$, 7 df, generalized linear model with linear link and variance proportional to the mean). This gives a hint of density dependence: rearing habitat could be limiting under some conditions, so when large numbers of fry emerge from the gravel only a small proportion can remain to rear above RBDD. This inference could be tested using otolith daily rings to determine whether length at age is a function of population size for the later emigrants. For the moment, because of some uncertainty in identity of the larger fish, density dependence remains only a suggestion.

A comparison of the emigration timing patterns at the different river locations shows how broad the range of dates can be, especially at RBDD where many more fish are caught than further downstream (because of greater effort and numbers of fish)(Figure 14). The successive median timing of passage at RBDD, GCID, Knights Landing, and the Sacramento trawl indicated a mean migration speed of 0.3 ± 0.05 km/day (95% CL), based on linear regression of location on river kilometer for all years when data were available from all four stations ($p < 0.0001$, 18 df). This fit did not improve if year was included as a factor (Akaike Information Criterion for the full model = 167, for linear regression = 166). Note that this migration speed is based on data for all size classes of fish together, which is strongly biased by the preponderance of small fish. Therefore this should be considered the migration speed of the smaller fish, which is orders of magnitude lower than typical river velocities of ~ 80 km d⁻¹ (Deas et al. 1997).

Migration speed for larger hatchery fish was determined from tagged winter Chinook released at LSNFH and recovered at various downstream locations (Figure 15). In 1998 the fish were released in April and achieved a median migration speed of 32 km d⁻¹. Otherwise median speeds

were $\sim 10 \text{ km d}^{-1}$ (Figure 15). These values are 1-2 orders of magnitude higher than those for smaller, wild fish determined above, but still below typical river velocities; the difference between fry and smolts may be an artifact of hatchery rearing, but is likely influenced by the migratory behavior of smolts as opposed to the drifting behavior of fry.

Growth rates of smolts from LSNFH, determined by robust regression of gain in length vs. time in the river, averaged $\sim 0.5 \text{ mm d}^{-1}$ (Table 6). These growth rates are similar to those reported by Sommer et al. (2001) for tagged fall Chinook in the Sacramento River and Yolo Bypass during January-February, although there were differences in length of the fish and duration of the migration period.

Catches in the beach seine survey for two years indicated a slightly earlier arrival in the lower river than did data from the Knights Landing screw trap or Sacramento trawl (see below). Catches in the beach seine were mainly confined to the Sacramento River, although sampling in most years was too late at most Delta locations to collect winter Chinook.

Median dates of key events in the winter Chinook life cycle (Figure 16) show the sequence of upstream migration, spawning, emergence, and passage of juveniles by various sampling points in the river. Beginning with emergence, the movement of juveniles during years when data were available from most sites suggests a fairly consistent pattern, except that in years before the screw traps were operated, the Sacramento River trawl data indicated a later passage. This may be an artifact of the much smaller number of fish collected during those years and the likelihood of contamination by fish from the much more numerous fall run (e.g., see Figure 11). Estimated passage from the Chipps Island trawl data is included here, mainly to reinforce the point that these data are unreliable because of the apparent contamination of the winter Chinook size class by other groups of fish (Figure 11). However, it is likely that migration speeds slow once the fish reach the estuary and net seaward flow decreases because of the increase in cross-sectional area.

The data presented above confirm that most winter Chinook exhibit an ocean-type behavior with respect to emigration timing (Healey 1994). The pace of movement of most of the winter Chinook is rather leisurely from the time they depart the spawning reach until they leave the Delta. Presumably a mean speed of 0.3 km d^{-1} indicates a saltatory movement by individual fish that spend most of their time foraging near shore. Because of ambiguity in the identity of larger fish, it is impossible to determine the proportion of fish that remain in the river beyond ~ 250 days from spawning.

There are no reports documenting feeding by juvenile winter Chinook during migration. It is reasonable to infer feeding habits from other runs of salmon, about which slightly more is known. Chinook generally feed on insect larvae and terrestrial insects in freshwater (Merz and Vanicek 1996, Sommer et al. 2001, Merz 2002), shifting toward zooplankton and larval fish in estuaries before becoming piscivorous in the lower estuary and ocean (MacFarlane and Norton 2002).

Estuary and Ocean

Winter Chinook pass through the San Francisco Estuary on their way to the ocean. Most of the interest in this passage has emphasized the Sacramento-San Joaquin Delta, because of the nexus of a listed species of fish with the keystone of two major water projects. Survival of winter Chinook through the Delta has been of great interest among resource agencies, because of the

wide concern that mortality of juvenile salmon is high in the Delta and that the water projects are responsible for a substantial fraction of that mortality.

Winter Chinook within the Delta are collected by the Sacramento (discussed above) and Chipps Island trawls and at the south Delta fish salvage facilities. The separation between the winter Chinook and other races in the Delta is ambiguous (Figure 11). In particular, groups of fish of length at date not seen in any of the Sacramento River samples are quite abundant in the salvage samples. Although attempts have been made to revise the length criteria specifically for use in the Delta, these have not solved the problem of the obvious overlap of different size groups (NOAA Fisheries 2004).

The timing of catch of fish within the winter Chinook size criteria at the state and federal salvage facilities in the south Delta, and at the trawl station at Chipps Island, appear rather invariant with a range of median dates of ~25 days for each site (Figure 17). The leakage of fish from other races (especially the more numerous fall run) across the size criteria results in contamination of the counts of winter Chinook, and bias toward a later time when the fall-run are more abundant. Our data therefore show only that the seaward migration of winter Chinook out of the Delta occurs in January-March, and that the captures of fish within the size criteria for winter Chinook occurs at about the same time in the fish salvage facilities and at Chipps Island.

Of the genetically identifiable fish collected at the fish facilities, 713 were provisionally identified as winter Chinook and 6039 were other races. Most of the winter Chinook fit within the size criteria for that run (Figure 18). However, only about half of the fish within the size criteria actually were winter Chinook (Hedgecock 2002). Furthermore, a small fraction of the winter Chinook appeared at the fish facilities at a length of ~100 mm before December, placing them well outside the size criteria. This pattern was also noted in samples taken in the lower Sacramento River and Delta (Hedgecock 2002). Thus, some winter Chinook are developing earlier than most of the run. Furthermore, the weak evidence for increase in size over time in the winter Chinook from these samples suggests that they are not remaining in the Delta for very long (Hedgecock 2002). Finally, these results demonstrate the inadequacy of the size criteria for distinguishing winter Chinook from other Chinook races in the Delta. Nevertheless, these data give similar estimates of emigration dates to those based on size criteria and show that winter Chinook leave the estuary at ~100-150 mm length.

Migration speed within the estuary based on recapture of tagged fish released at Ryde or Isleton (Figure 2) is weakly related to river flow (Figure 19). At flow below ~20,000 m³ s⁻¹ migration speeds cluster around 4 km d⁻¹, and only at higher river flows do migration speeds increase. This suggests some directed movement in the seaward direction which may be aided by river flow. These speeds were considerably less than those determined from difference in peak time of passage of tagged fish from LSNFH recovered in Sacramento and at Chipps Island. This may be because the LSNFH fish were already accustomed to migration, whereas the fish released in the Delta were naïve. If so, this has implications for the interpretation of both the coded-wire-tag experiments in the Delta and the movements of radio-tagged fish.

No data are available on the movements of winter Chinook after they leave the Delta. Fall Chinook smolts migrated through the lower estuary in ~ 40 d, at a rate of ~ 1.6 km/day, based on mean ages at the mouth of the estuary and at km 68 (MacFarlane and Norton 2001). Most winter Chinook enter the ocean during their first year of life. There is little information on their movement and distribution once they reach the ocean. Chinook salmon in the ocean feed on

micronekton including fish, euphausiids, and squid (Hunt et al. 1999, MacFarlane and Norton 2002).

Effects of the export pumps The water export facilities in the south Delta can take a substantial fraction of the Delta's freshwater inflow and are therefore a major concern for management of salmon and other fish that use the Delta. For winter Chinook the principal effect of the water export facilities would be that fish go to the facilities during migration, either because they are acting passively or because the flow patterns in the Delta do not provide clear cues to allow them to migrate toward the ocean.

Unknown
1) Four issues preclude a clear analysis of the effects of the export pumps on winter Chinook. The first is the ambiguity about the identity of each unmarked fish discussed above. The second is that some fraction of the salmon that moves toward the fish facilities never get there, presumably
2) because of predation in the waterways leading to the fish facilities. These losses of fish have been estimated as high as 95% for the state facility (Gingras 1997), although a value of 75% is generally used to estimate the losses attributable to pumping (Kimmerer and Brown 2006). The predatory loss at the federal facility is unknown, and a value of 15% has been used as a placeholder with no real justification. The third issue is that the fish that are salvaged and
3) returned to the estuary have an unknown post-salvage survival, which may be low because of attraction of predators to the release site (D. Odenweller, CDFG, retired, personal
4) communication). The fourth is that the actual number of winter Chinook migrating through the Delta is unknown, so even with reliable information on the number lost to the effects of export facilities, the population-level impacts of those losses would be difficult to estimate.

The proportion of winter Chinook estimated to have been lost at the fish facilities, based on recovery of tagged fish released at Livingstone Stone National Fish Hatchery (LSNFH), was 0.3 – 6.5% of the total tagged fish leaving the estuary (Table 7). This proportion was unrelated to Sacramento River flow, export flow, and the number of tagged fish recovered at all locations. The median estimated percent survival from LSNFH to departure from the Delta was 2.8% (Table 7).

Survival through the Delta The U.S. Fish and Wildlife Service has sampled and investigated Chinook salmon in the Delta since 1976 using trawls and beach seines (discussed above), mark-recapture studies, and other approaches (Kjelson and Brandes 1989, Kjelson et al. 1982, Brandes and McLain 2001). Brandes and McLain (2001) presented detailed information on migration pathways, potential environmental factors, distribution, abundance, and survival in the Delta. Most of this work has focused on migration of fall Chinook smolts through the Delta, although some of the conclusions probably apply to winter Chinook. Chinook salmon pass through the Delta via the Yolo Bypass during flood conditions, by the Sacramento River mainstem, through Sutter or Steamboat Sloughs on the west side of the Sacramento River, and by entering the central Delta through the Delta Cross Channel (DCC, when gates are open), Georgiana Slough, Three-Mile Slough, or the confluence with the San Joaquin River (Figure 2). Once in the central Delta, the fish are at risk of entrainment in the south Delta water export facilities, and survival of fish that enter the central Delta is lower than survival of fish that remain in the Sacramento River (Brandes and McLain 2001).

Many factors affect survival as determined from these experimental data, and analysis is sufficiently challenging to have resulted in several publications in the statistical literature. The first analysis applied a ridge regression, including a large suite of potential explanatory variables

identified by fish agency scientists (Newman and Rice 2002). Water temperature was the most important variable (see also Brandes and McLain 2001). The variables of greatest management interest either contributed little to the fit of the model (ratio of export flow to inflow), or had ambiguous effects (Newman and Rice 2002). For example, river flow had a positive effect on survival but so did salinity, which decreases with increasing flow, suggesting a nonlinear influence. The position of the Delta Cross Channel Gates had an effect but the sign of that effect depended on the release site. A particle-tracking model study showed no effect of DCC gate position on the fraction of particles released in the Sacramento River above the DCC that ended up at the export facilities (Kimmerer and Nobriga, in prep).

Most analyses of survival of winter Chinook through the Delta have used coded-wire-tagged late-fall Chinook from the Coleman hatchery as surrogates. The degree of similarity between the behavior and survival of these fish and that of naturally-spawned winter Chinook is unknown. Most of the experimental emphasis has focused on the relative survival between paired groups of fish released in Georgiana Slough and at Ryde on the Sacramento River just downstream from Georgiana Slough, (Figure 2), and recaptured in the Chipps Island trawl or in the ocean fishery. Regressions of this survival ratio on export flows averaged over the 3 days after release are significant for the ocean recaptures but not quite for those at Chipps Island (Figure 20, Table 8). However, export flows were rarely steady after the releases (Figure 20), and regressions using longer averaging periods are less significant (Table 8). Effects of temperature have also been noted in these data (B. Manly, pers. comm.). We found no relationship between temperature from the Rio Vista continuous monitoring station averaged over 10 days after release and the survival ratio based on ocean recoveries, but the relationship for the Chipps Island recoveries was significant ($p < 0.02$, 12 df). However, this result vanishes if a single point is deleted, so it is not very robust.

Taken as a whole the results of the above analyses, particularly those of Newman and Rice (2002) and Newman (2003), suggest that flow and export conditions in the Delta affect survival, but also that the number of uncontrolled variables is probably too large to allow for unambiguous interpretation of these mark-recapture data. Furthermore, few of the mark-recapture studies have addressed the question of overall survival, or of which pathway the fish take under different conditions. The studies using late-fall Chinook in particular have been narrowly focused on comparing survival in two parts of the system. Thus, after several decades of mark-recapture studies, the fundamental question being addressed, that of the effects of flow and export conditions on survival of salmon migrating through the delta, remains unanswered.

Harvest

Chinook salmon, including winter run, are harvested in recreational and commercial fisheries off the coasts of California, Oregon, Washington and British Columbia. The Pacific Fisheries Management Council (PFMC) manages the U.S. commercial fisheries under a Fisheries Management Plan (FMP). A Biological Opinion issued by NOAA in 1996 concluded that the ocean fisheries did not contribute to the decline of winter Chinook but that the fisheries may be reducing its chances of recovery. Responding to the Opinion, the PFMC took measures to reduce the winter Chinook harvest fraction by 50%, including changes in opening times and minimum length (see for example, PFMC 2002).

About 82% (range 73 - 100%) of tagged fish from LSNFH recovered in the ocean were caught in the sport fishery (Table 9). This can be attributed to the difference in fishing regulations

between the two fisheries. The commercial season begins later (July in 1997-1999, late May in 2000-01, 1 May in 2002-3) than the sport fishery (mid-April starting in 2000). The minimum length of fish that may be retained in the fisheries is 26-27 inches for commercial trollers and 20 inches for sport anglers. The distribution of tag recoveries depends on the joint distributions of the fish and the fishery, which is governed by regulations, economic factors, and the distribution of the more abundant fall Chinook. During February to May of 1995 - 2002, on average 6% of the sport effort was recorded at Fort Bragg, 36% at San Francisco, and 58% at Monterey (PFMC 2004); respective percentages for the LSNFH tag recoveries are 1%, 51%, and 48%.. These limited data suggest a concentration of the fish near San Francisco and south, at least during the few months leading up to migration.

Chinook salmon caught in the ocean fishery are not routinely identified to run except by tag recoveries. Since the fall run is much more numerous than the others, most of the fishery data apply to it and the fishery impact on winter Chinook is obscured. However, by using results from six studies of tag recovery, we have estimated fishing mortality on winter run (Figure 21). Fishing mortality varied around ~50% during most of the period of record, and is now ~20%. The harvest of winter Chinook is somewhat lower than that of fall Chinook because of the factors discussed above. The revision to the harvest regulations appears to have resulted in a substantial reduction in the ocean harvest of winter Chinook salmon.

In-river harvest of winter Chinook was estimated at 8.7% of the run during 1983 - 1986 (NOAA Fisheries 1997). Since 1987 the California Fish and Game Commission has restricted inland harvest of adult winter Chinook. At present the year-round closure to salmon fishing between Keswick Dam and Deschutes Road Bridge (near Anderson) and additional rolling closures between the estuary and the Deschutes Road Bridge have essentially eliminated the inland recreational harvest of adult winter Chinook. Since 1992, incidental mortality to juvenile winter Chinook was reduced significantly by restricting the use of barbs and the size of hooks used by Sacramento River trout anglers and by prohibiting salmon being removed from the water. In combination, these changes in fishing regulations have probably nearly eliminated the impact of the recreational harvest on winter Chinook.

Management

The cohort replacement rate (CRR) changed from a long-term average of 76% before ~1993 to 145% after, a near doubling. Why did this happen? Several more or less concurrent management actions combined to effect this change, but how much effect did each have? We explored this question through a rather simplistic model; Baker et al. (in prep) are using a state-space model to integrate and better quantify the effects of these actions together with changes in spawning habitat and other environmental variability. The state-space model developed by Newman and Lindley (2006) did not cover the entire time period, nor did it allow for step changes in relationships between environment and salmon survival.

The least reliable part of our model is the estimate of thermal mortality, because of the need to reconstruct river temperature and the uncertainty in the model of survival as a function of temperature. All four alternative approaches to this problem are compared in Figure 8. These results are consistent in showing no survival in 1977, poor to none in 1976, moderate and variable survival in 1978 – 1993, and high survival thereafter. Generally the threshold models resulted in higher survival, particularly in the later years when spawning occurred higher in the

river and temperatures in those reaches did not exceed 16°C. However, correlations among these survival estimates ranged from 0.85 to 0.94, and the single free parameter in the model results in relatively little difference among these alternative formulations.

The model including effects of hatchery production, harvest, changes in redd distribution, and temperature effects gave cohort replacement rates (CRR) that generally tracked those estimated from the population data, although with much less variability (Figure 22). The effect of severe thermal effects is clear in both the data and the model output in 1977 and to a lesser extent 1976. The effect of high temperature in 1977 was stronger in the model than in the data, presumably because the model included only fish from a single year class to account for recruits 3 years later. The general trend in CRR values is similar in both model and data, with most values >1 since the 1990s. The correlation between modeled and measured log-transformed CRR values was 0.66, and 0.63 excluding 1977 which had a strong influence on the correlation. The substantial variation not captured by the model could be due to measurement error or random variation, but could also represent some real additional environmental influence not in the model.

The largest effects of management were due to harvest reduction and the combined effects of RBDD and ACID operations and temperature control on thermal mortality. Hatchery inputs had modest effects. Analysis of available environmental variables did not suggest a strong additional influence on the overall trajectory or interannual variability of winter-run Chinook salmon. Regression parameters relating environmental variables to model residuals all had confidence limits that included zero, with one exception (Figure 23). This exception was the number of days during which temperature at Keswick Dam exceeded 16 °C. This regression was strongly driven by data from brood year 1977, presumably due to our neglecting age classes other than 3 years; without that point the relationship is non-significant.

Otherwise none of the environmental variables had a significant effect on the trajectory of residuals from the model. This can be interpreted in several ways. First, a particular environmental variable may have no effect. Second, the effect may be small and lost in the variability in the data. Third, the effect may be substantial but correlated with the effects that were included, such as to mask a real effect. For example, RBDD gates were opened during part of the downstream migration starting in 1992 and for most of the migration starting in 1994. The effect of this action could be hidden by those of harvest and particularly temperature control. The thermal model could be too sensitive, so much of the mortality attributed to temperature may have been actually due to effects of the dam on downstream migrants. Until a better model of temperature effects on survival can be developed, we have no way to tell.

However, most of the other environmental variables have patterns of variation unlikely to be confounded with those in the model. In particular, conditions in the Delta have not undergone a change consistent with the reversal in trend of winter-run salmon. Furthermore, ocean conditions, at least as represented by the selected indices, do not appear to have contributed to the change in CRR of winter-run salmon. This contrasts with the situation for other salmon stocks which respond strongly to ocean conditions (e.g., Hare and Francis 1995, Mantua et al. 1997).

River flow is also considered a key variable in managing salmon populations, and it is a strong predictor of recruitment for San Joaquin Chinook (Speed 1993). However, relationships to flow appear to be weak for Chinook from the Sacramento basin, and we found no effect of flow on winter Chinook. The upper mainstem Sacramento River is relatively steep-sided, so perhaps

there is little change in habitat conditions with flow as might occur in rivers with a more gradual bank slope.

This model leaves out any consideration of physical habitat, yet it is clear from the stock-recruit curves (Figure 9, see also Newman and Lindley 2006) that the quantity of physical habitat must be substantially lower now than it had been in 1967 – 1978 (F. Ligon, pers. Comm., Baker et al. in prep.). Since the opening of the area above ACID, additional habitat has been made available but the data have been too variable to develop stock-recruit relationships. The very large adult return in brood year 2002 produced fewer adults three years later than would be expected, suggesting habitat limitation.

In retrospect we are surprised that many millions of dollars were spent to reduce temperature at Shasta Dam without a concerted effort to quantify mortality processes. Not only were daily temperature data unavailable for much of the river over much of the historical record, but no mathematical model of thermal mortality had been developed. The experiments we used to develop our model were conducted after the temperature control device was in place, and were not designed, or particularly suitable, for model development.

We have been able to tease out the likely factors contributing to the increase in CRR of winter-run salmon because of the extraordinarily strong signal-to-noise ratio in the data. No doubt these results will be controversial, but the fact remains that these data have a story to tell. We believe that this may be a fairly rare instance in which it is possible to estimate the effects of management actions from abundance data. In most cases this will not be possible because of the low signal-to-noise ratio, and inferences will have to be drawn from investigations at a more mechanistic level than provided by monitoring data.

Conclusions

Future of winter Chinook

Winter Chinook will probably remain at some risk of extinction (NOAA 2003, Good et al. 2005, Lindley et al. 2006). There is only one winter Chinook population, its spawning area is restricted and vulnerable to high temperature in droughts, and age at maturity is limited. Although restoration of Battle Creek may provide a hedge against extinction of winter Chinook in times of drought (Brown and Kimmerer 2004), the use of that habitat by spawning winter Chinook has yet to be demonstrated.

Small salmon stocks have a relatively high risk of extinction that can be difficult to predict because of random fluctuations (Routledge and Irvine 1999). Botsford and Brittnacher (1999) examined the probability of quasi-extinction based on estimates of adult winter Chinook passing Red Bluff Diversion Dam (RBDD) up to 1995; quasi-extinction refers to a model population falling below a specified level, taken to be 100 female spawners. Their model assumed no density dependence, which they justified because of the small size of the population. Using this model they showed that winter Chinook had a high probability of quasi-extinction, and determined delisting criteria: at least 10,000 female spawners, with a geometric mean cohort replacement rate of at least 1, over a 13-year period and assuming that the error in estimating population size did not exceed 25%. However, the model of Botsford and Brittnacher (1999) had a temporally invariant cohort replacement rate, which did not allow for the possibility that actions taken to protect winter Chinook might allow the population to increase. Lindley and

Mohr (2003) examined the effect of predation by striped bass, including effects of stocking striped bass, on the probability of extinction, based on data through 1996. Their Bayesian model was slightly more complex than that of Botsford and Brittnacher (1999), and it included a step change in population growth rate reflecting the various conservation measures that were taken in the early 1990s. Nevertheless, the probability of quasi-extinction was still high, particularly if the striped bass population were allowed to increase (Lindley and Mohr 2003). The cumulative effect of the conservation measures was large, although there were only a few years of data available after these measures had been taken.

Estimated extinction risk is sensitive to the rate of population growth (modeled here as cohort replacement rate). The recent positive rate of growth results in a near-zero extinction risk (Good et al. 2005), but this ignores risks of catastrophe not experienced during the recent time of population growth, as well as the possibility that the population has reached carrying capacity and will not grow further.

In this paper we have examined the influence of management actions on density-independent factors, but density-dependent survival of eggs and alevins could now be limiting the increase in the population size. If that is true, the spawning population under current management may remain below the proposed recovery target of 20,000 spawners.

Projections of saturation or continued increase in spawning population assume that thermal conditions in the river will continue as they have since temperature control measures were introduced in the mid-1990s. However, these measures rely on the availability of a large cold-water pool in Shasta Reservoir. A protracted drought or a sudden demand for water, for example following failures of multiple levees in the Delta (Mount and Twiss 2005), could reduce or eliminate that cold-water pool, and temperature in the river would again rise to lethal levels. Thus, the risk to winter Chinook has two parts: one part related to demographic and environmental variability such as that captured by the models discussed above, and the other related to climate variability and the probability of catastrophes or protracted droughts. Although droughts are predictable in a stochastic sense (which is suitable for risk analysis), we do not know whether the management response to droughts of various lengths can be forecasted.

Climate change presents an additional reason for concern about the future of winter Chinook (Lindley et al. 2006). Although predictions of future precipitation in California are variable, the temperature trend is clearly upward (Roos 1989). This will shift the runoff peak earlier in the season (Roos 1989), which has already been noted (Dettinger and Cayan 1995). The cold-water pool in Shasta Reservoir will be more difficult to maintain during future droughts that coincide with higher temperature and earlier, warmer runoff. Other risks with low probability but possibly catastrophic impact include volcanic activity at Mt. Lassen, a toxic spill, or a disease outbreak (Lindley et al. 2006).

Actions to protect winter Chinook

Based on our analyses and observations, several actions are necessary to protect winter Chinook, and additional actions may be necessary to restore them to the level at which they may be delisted.

Harvest The harvest fraction of winter Chinook is now lower than it has been in the last 3 decades. We cannot say whether it would be feasible or advisable to lower it still further, since that decision involves all other Chinook runs as well as social and economic factors. Still, it is a

straightforward observation that spawning runs will vary inversely with the harvest fraction, and allowing it to increase will decrease the number of adults going up the river. The impact of that increase depends on whether carrying capacity has been reached.

Temperature control Installation of an elaborate temperature control device allowed the release of cool water from Shasta Dam without forgoing power production. This will continue to be effective as long as the cold-water pool is available in Shasta Reservoir, which depends on water management and droughts, and therefore also on future climate.

Dams Keeping the RBDD gates open for much of the spawning migration continues to be a highly effective strategy, principally by allowing the salmon to migrate as far upstream as possible to spawn. Having the gates open during downstream migration may also be a benefit, although we cannot quantify it.

Improving the fish ladders on ACID allowed the winter Chinook access to additional spawning grounds. However, the fraction of fish spawning above ACID has been increasing, and in 2005 it was over 50%. The relatively small amount of spawning habitat above ACID (F. Ligon, pers. Comm.) may be saturated at current population levels, while other suitable habitat downstream goes unused.

If the next few years of data on run size suggest that the population abundance has reached a carrying capacity, consideration should be made of blocking access above ACID for part of the run. This should be done at first in an experimental mode in which close observations of spawning populations and superimposition are combined with controlled access above ACID, alternating by year between high and low access.

Gravel augmentation: Likewise, saturation of habitat would suggest that spawning gravel is limiting population growth. Ligon et al. (in prep.) show the paucity of spawning habitat even with the gravel augmentation that has occurred. The extent of suitable habitat should be monitored on a regular basis, and additional gravel added when needed.

Hatchery production: At current production levels the LSNFH contributes a moderate amount to the recovery of winter Chinook. More important than this contribution, though, is that the hatchery is a way of hedging against the complete loss of one or more year classes due to drought and resulting high temperature or other calamities. On the other hand, the contribution of hatchery-reared fish to the population spawning in the river has been increasing, possibly raising the risk of extinction (Lindley et al. 2006). The hatchery should be evaluated to ensure that it provides a robust and conservative hedge against likely scenarios based on climate and water management. The hatchery should continue to mark all winter Chinook produced.

Delta Although considerable effort has been devoted to understanding and correcting problems with Chinook movement and survival through the Delta, the available evidence does not support a strong influence of water operations in the Delta on the overall survival of winter Chinook. Furthermore, none of the current efforts at investigating these effects is designed to show what these effects are, although they are designed to examine pieces of that question. Until that level of understanding can be developed, it seems advisable to keep export flow as low as feasible during the winter Chinook migration season. Delta Cross-Channel gates should be kept closed when water quality in the Delta permits, although the benefits to the winter Chinook population has not been conclusively shown and particle-tracking model results do not suggest benefits are large.

A substantial impediment to understanding the role of the Delta in the life of winter Chinook is our inability to distinguish winter Chinook from other runs. Without a systematic, well-reported system of genetic identification, it is impossible to determine the timing of migration through the Delta, or the abundance of winter Chinook at any part of their migration. Such a program would allow for a substantial improvement in management practices and the response of the population to those practices.

Research needed

A substantial amount of valuable information is available for winter Chinook. Several areas of research would greatly improve our understanding as it relates to management.

Temperature effects The most critical need is a quantitative understanding of temperature effects on winter Chinook eggs and alevins. Research to develop this understanding should combine modeling and experiments that explore both constant and varying temperature and include the effect of exposure time. The result should be a predictive model of how survival of a group of winter Chinook varies as temperature fluctuates through the summer. This is a challenging task and has never been done before for any fish species as far as we know. However, winter Chinook is most threatened by future increases in temperature. Understanding that threat in quantitative terms should be the primary goal of research on this fish.

Future conditions: An effort to model the interaction of water project operations with climate would be helpful in forecasting the risk of future high-temperature events. In combination with a revised model of thermal mortality, this kind of forecasting could be used to evaluate risk and to devise alternative mitigation strategies. To the extent that catastrophes in the Delta are likely to increase water demand, models should include this possibility as well.

Genetic sampling: The only way to reliably distinguish winter Chinook from other Chinook at some life stages is through genetic testing. Current methods appear adequate for distinguishing winter Chinook from other races. However, fish for genetic analysis have been collected in an apparently haphazard sampling program, the genetic data are not widely available, and the records on tissue sampling are apparently unavailable. This program should be replaced by a program of systematic, stratified random sampling and subsequent genetic testing in a suitable production facility. The fraction of the population sampled should be increased as the cost of analyses falls. The data on sampling and results should be made available online, as are most other data in the Central Valley.

Delta investigations The current efforts at assessing survival of winter Chinook in the Delta should be replaced by a program specifically designed to answer the key questions: what is survival, and how is it affected by water project operations and other factors? The design for this program should be peer-reviewed, perhaps through a competitive process.

Monitoring: The current level of monitoring is quite impressive and seems adequate for tracking the abundance of winter Chinook. Since all of the hatchery fish are tagged, separating hatchery from naturally-spawned fish is easy. If a consistent, well-designed program of genetic analysis were to be developed and applied, the monitoring program would be greatly improved especially in the Delta. Still, the suggestions of Lindley et al. (2000) should be revisited regarding power analysis for monitoring to detect and verify recovery for delisting.

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Table 1. Hatchery production by broodyear. Sources are the Coleman National Fish Hatchery (CNFH) and Livingstone Stone National Fish Hatchery (LSNFH) , and captive broodstock program at Bodega Marine Laboratory and Steinhardt Aquarium. Data sources: USFWS 2001, CDFG 2002, 2004.

Brood Year	Released	Source
1991	11582	CNFH
1992	27404	CNFH
1993	19721	CNFH
1994	44008	CNFH
1995	51915	CNFH
1996	4718	Captive Broodstock
1997	31337	Captive Broodstock
	20846	LSNFH
1998	147393	LSNFH
1999	30436	LSNFH
2000	162198	LSNFH
2001	244829	LSNFH
2002	222323	LSNFH
2003	216745	LSNFH
2004	169261	LSNFH
2005	163218	LSNFH

Table 2. Sources and attributes of data used in this paper. BDAT, Bay-Delta and Tributaries database (<http://bdat.ca.gov/>); CDEC, California Data Exchange Center (<http://cdec.water.ca.gov/>); CDFG, California Department of Fish and Game; GCID, Glenn Colusa Irrigation District diversion; PFMC, Pacific Fishery Management Council (<http://www.pcouncil.org/>); RBDD, Red Bluff Diversion Dam; USFWS, U.S. Fish and Wildlife Service.

Life stage / Variable	Sampling program	Time period	Years used	Source	Remarks
Temperature	Keswick Dam monitoring	Daily	1989 – 2005	CDEC	
Ocean harvest	Central Valley harvest estimate	Annual	1970 - 2004	PFMC	Not specific to winter Chinook
In-River harvest	Variable	Annual	1972 – 1993	Mills and Fisher 1994	Harvest assumed zero after 1993
Adult migrants	RBDD fish ladder counts	Week	1967-2004	D. Killam, CDFG	Dam gates open since 1986; counts expanded using 1982-1986 timing
Adult spawners	Carcass surveys	3-day periods	1996-2004	D. Killam, CDFG	Petersen and Jolly-Seber estimates differed somewhat when both were calculated
Redds	Aerial redd surveys	Variable; >10 surveys after 1992	1982, 1985, 1987-present	D. Killam, CDFG	
Juvenile migrants	Sampling to determine salmon race based on genetic markers		1996-2001	D. Hedgecock, UCSC	No metadata
Juvenile migrants	RBDD screw trap counts	Daily (weekdays)	1994-1999, 2002-2004	W. Poytress, USFWS	
	Knights Landing screw trap counts	Weekly summary	1995 – 2004	M. Brand, CDFG	
	GCID screw trap counts	Daily (weekdays)	1996 – 2004	BDAT	
	Sacramento River trawl survey		1988 - 2004	BDAT	Midwater or Kodiak trawls
	Beach seine		1977 - 2004	BDAT	

	Chipps Island trawl survey		1976 – 2004	BDAT	Midwater trawls
	Salvage at fish facilities	Daily (most days)	1997 - 2004	BDAT	

Table 3. Summary of temperature reconstruction. For each station the table gives the location (from upstream down in river kilometers), the number of data points deleted, the number of data points remaining after cleaning up, the residual standard error of the regression of predicted vs. observed values, and the number of years with at least one data point, with the first year in parentheses (last year 2001 except as indicated).

Station	River Km	Deleted	Data Points	Residual SE (°C)	Years
Keswick Dam	486	1	3653	0.78	14 (1988)
Balls Ferry	444	-	4211	0.63	14 (1988)
Jelly Ferry	428	-	2324	0.63	10 (1988)
Bend Bridge	414	10	6024	0.75	21 (1970)
Red Bluff Dam	391	-	1048	0.54	4(1988 - 1991)
Tehama	369	56	3685	0.50	12 (1990)
Woodson	351	-	4281	0.53	14 (1988)
Hamilton City	320	50	4573	0.42	14 (1988)
Butte	270	-	3821	0.80	12 (1990)
Colusa	230	29	3751	0.81	17 (1975)
Grimes	201	1	11129	0.87	32 (1970)
Above Colusa Drain	145	60	3848	0.88	12 (1990)
Knights Landing	137	1	2695	1.17	12 (1990)
Verona	127	-	1260	1.43	6 (1979 - 1998)
Freeport	76	1	9114	1.38	27 (1975)
Hood	61	-	1043	1.10	3 (1999)

Table 4. Actions taken to protect winter-run Chinook salmon. Actions are numbered for reference and are not in any particular order. "Quant." refers to whether or not the effect can be quantified in absolute terms, i.e., numbers or proportions of fish: Yes, No, or Estimate.

No.	Action	Mechanism	Quant.
1	Reduce Shasta outlet temperature	Reduce thermal mortality to eggs and alevins	E
2	Open RBDD gates during spring	Improve passage for adults, reduce blockage and allow more to spawn in water that stays cool	Y
3	Open RBDD gates during fall	Reduce passage mortality to juveniles	N
4	Reduce toxic inputs at Spring Creek below Keswick Dam	Reduce toxic mortality to juveniles	N
5	Keep Delta cross-channel gates closed during downstream movement	Reduce mortality by keeping most fish in Sacramento mainstem rather than interior Delta	E
6	Reduce export flow during migration times of winter-run salmon	Reduce mortality of those fish that leave the mainstem Sacramento River	E
7	Add hatchery fish	Boost production	Y
8	Reduce harvest	Lower fishing mortality	Y
9	Revise ACID configuration and operations	Improve passage for adults, reduce variation in releases of water from Keswick Dam to accommodate ACID operations	Y (adult passage only)

Table 5. Environmental variables used in the analysis, along with data sources and results of regression analyses on residuals from the model. Flows in $\text{m}^3 \text{s}^{-1}$, temperatures in Celsius.

Variable	Season	Source	Slope \pm 95% CL
Flow at RBDD ($\text{m}^3 \text{s}^{-1}$)	Sep - Dec	USGS gaging data	0.0003 ± 0.001
Sacramento River flow at Freeport	Dec - Mar	DWR Dayflow program	0.0001 ± 0.0003
Export flow in south Delta	Dec - Mar	Dayflow	0.002 ± 0.003
Delta Cross Channel gates (0 for closed, 2 for both open)	Dec - Mar	Dayflow	-0.09 ± 0.27
Cross-channel flow	Dec - Mar	Dayflow	-0.001 ± 0.004
Cross-channel:Sacramento River flow	Dec - Mar	Dayflow	-0.7 ± 1.8
Gates open at RBDD	0 before 1992, then 1		0.2 ± 0.4
Mean summer temperature	Jun - Oct	T reconstruction	-0.04 ± 0.16
Max summer temperature	Jun - Oct	T reconstruction	-0.006 ± 0.12
Days of $T > 16$	Jun - Oct	T reconstruction	0.03 ± 0.01 0.01 ± 0.016 (less 1977)
Multivariate ENSO index	Jan-Jun	http://www.cdc.noaa.gov/~kew/MEI/mei.html	-0.05 ± 0.17
Pacific Decadal Oscillation Index	Jan-Jun	Mantua et al. 1997	0.06 ± 0.18

Table 6. Estimated growth rate (mm d^{-1} with 95% CL) of marked winter Chinook released at LSNFH and recovered downstream, based on robust regression of gain in length vs. days in the river (Figure 11).

Year	Growth rate	N
1998	0.59 ± 0.21	17
1999	0.38 ± 0.03	54
2000	0.46 ± 0.46	7
2001	0.54 ± 0.09	14
2002	0.37 ± 0.04	37
2003	0.46 ± 0.05	96

Table 7. Recapture of tagged winter Chinook released from the Livingstone Stone National Fish Hatchery. Catch is the total catch reported for all sample periods (fish facilities) or from the Chipps Island trawl during the time over which 99% of the fish were recaptured. Fish Flux is an estimate of the total number of fish that left the Delta during that time period.

Brood Year	Tag Codes	Number Released	Catch			Fish Flux	Percent Survival	Percent of Release			Percent Loss
			SWP	CVP	Chipps			SWP	CVP	Chipps	
1998	17	147393	8	0	20	3914	2.8	0.02	0.00	2.0	3.5
1999	5	30436	1	0	3	434	1.5	0.09	0.00	8.0	3.8
2000	8	162198	2	0	7	2159	1.4	0.03	0.00	4.6	2.0
2001	15	244829	2	2	23	2599	1.1	0.00	0.00	0.3	1.5
2002	26	222323	26	12	33	12354	5.9	0.02	0.02	1.9	3.8
2003	26	216745	26	5	21	7367	3.7	0.04	0.02	2.0	6.5
2004	13	169261	1	1	20	6795	4.0	0.00	0.00	2.8	0.3

Table 8. Regression statistics for mark-recapture studies using late-fall Chinook as surrogates for winter Chinook. In each regression the dependent variable is the ratio of survival indices for releases in Georgiana Slough to releases in the Sacramento River below Georgiana Slough. The independent variable is export flow averaged over either the 3 days or the 10 days following the release.

Recovery Point	Averaging period	Slope \pm 95% CL	p	df	r ²
Chipps Island trawl	3	-1.1 \pm 1.2	0.06	12	0.3
	10	-0.7 \pm 1.2	0.21	12	0.1
Ocean fishery	3	-1.7 \pm 1.6	0.04	9	0.4
	10	-1.3 \pm 1.6	0.10	9	0.3

Table 9. Expanded Ocean sport and commercial fisheries recoveries of coded wire tagged winter Chinook released from Livingston Stone National Fish Hatchery, by broodyear. (Data from the Pacific States Marine Fisheries Commission's Regional Marking Information System data base.)

Fishery Management Area	Brood Year										Totals	
	1998		1999		2000		2001		2002			
	Sport	Comm.	Sport	Comm.	Sport	Comm.	Sport	Comm.	Sport	Comm.	Sport	Comm.
British Columbia	7										7	
Washington												
Northern Oregon	3										3	
Coos Bay, OR	4								5		5 4	
Klamath Mgmt. Zone (OR)	3										3	
Klamath Mgmt. Zone (CA)	4								4		8	
Fort Bragg			8						4 8		12 8	
San Francisco	33		27 11		27 18		31		374 75		492 104	
Monterey	86 15		32		41 7		14		290 66		463 88	
Total	126 29		67 11		68 25		45		677 149		983 214	

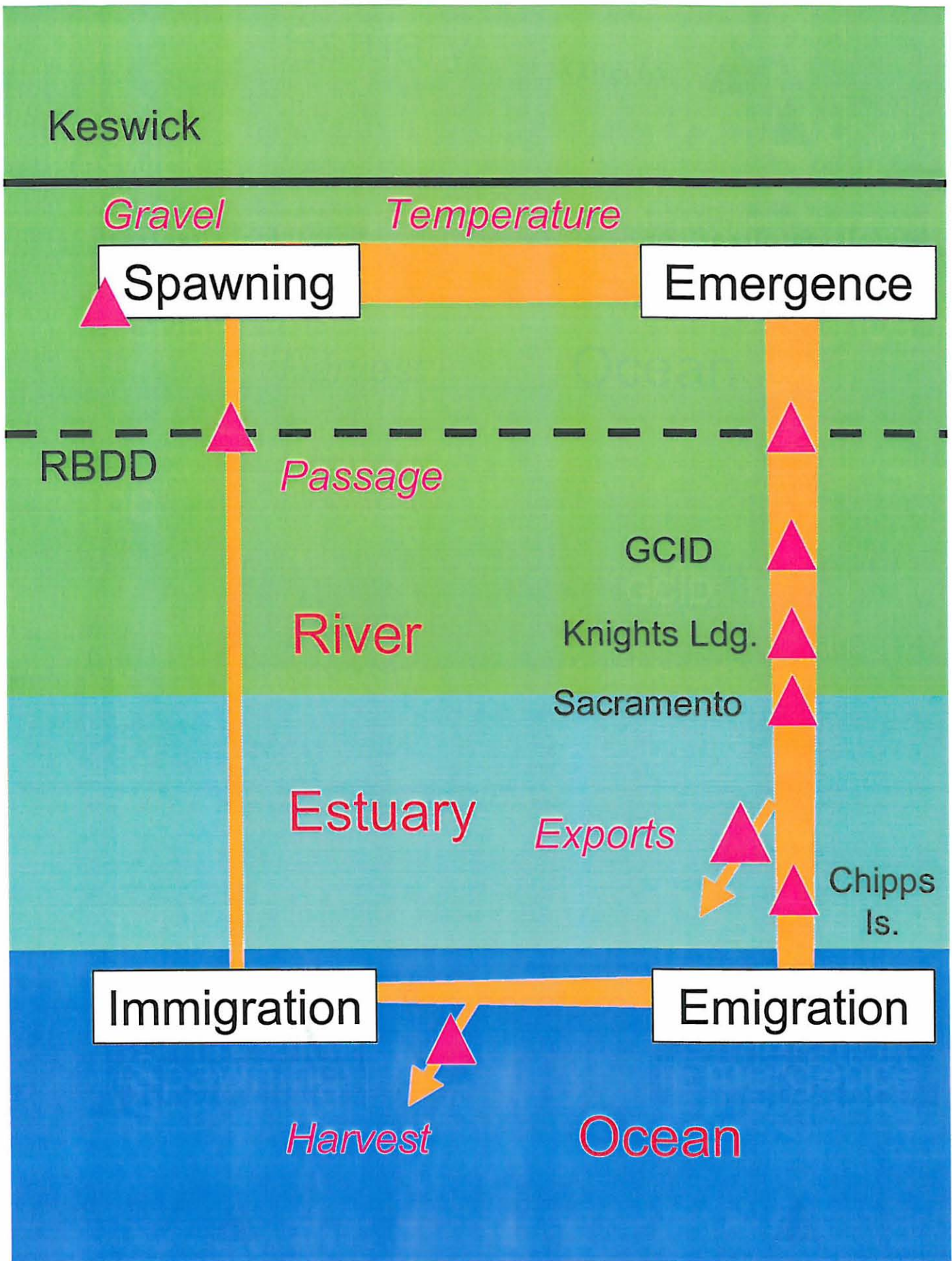
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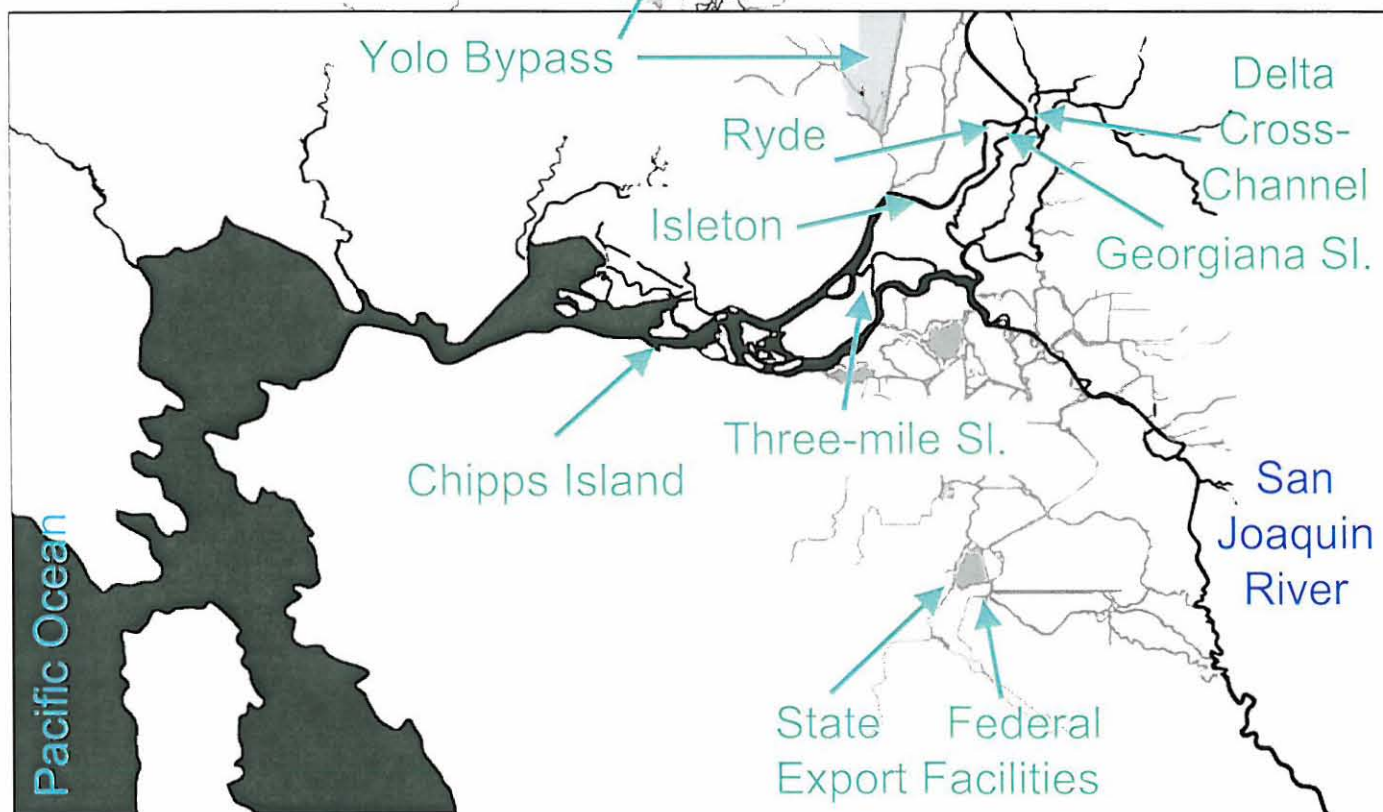
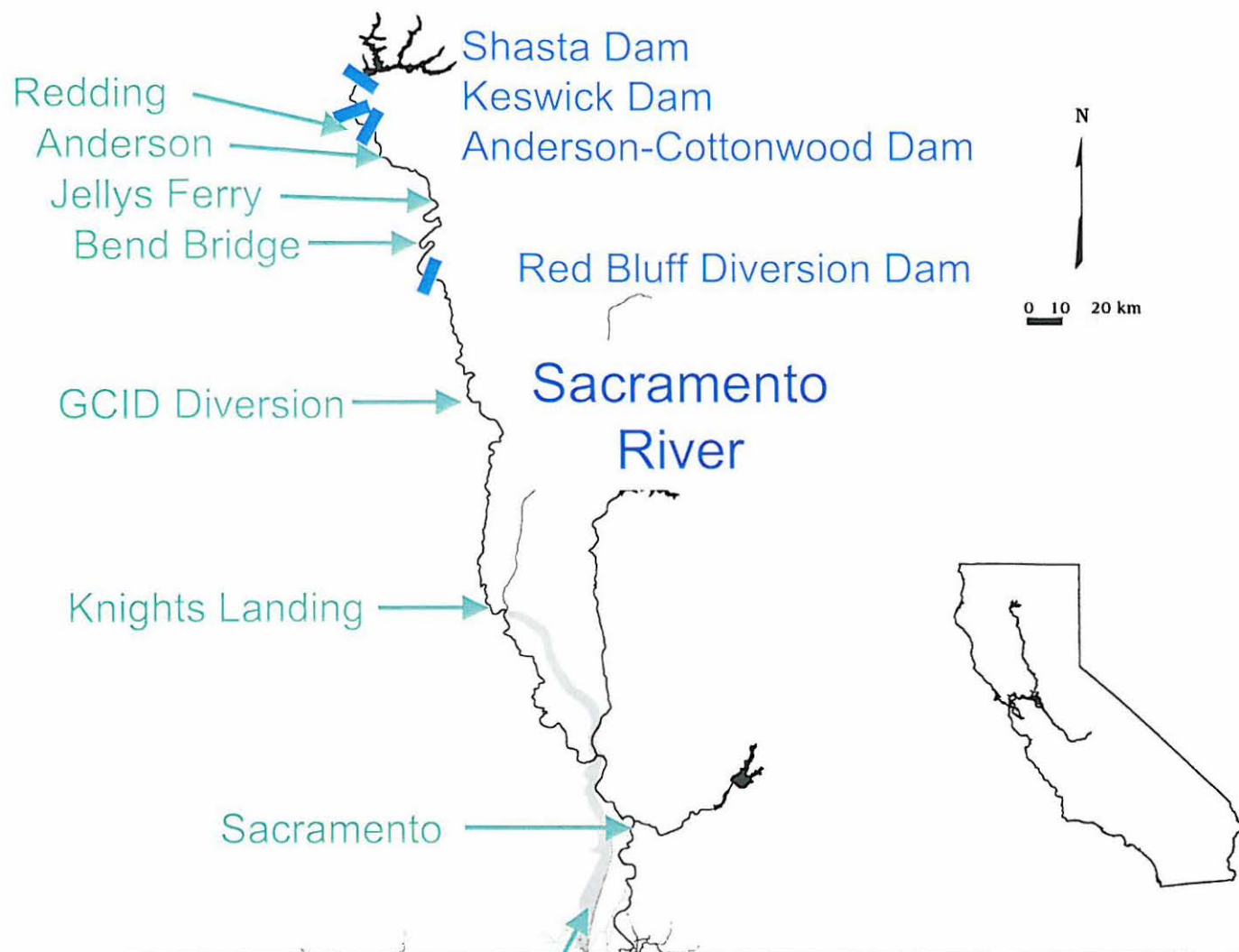
1. Schematic diagram of the life cycle of winter Chinook salmon. The orange line represents the number of fish progressing between successive life stages, and the width of the line is scaled to the estimated mean log abundance of that stage in recent years. This is superimposed on a schematic map of the system, with triangles indicating locations where observations of winter Chinook are made. Text in italics indicates key environmental issues for winter Chinook.
2. Map of the Sacramento River showing the current winter Chinook spawning distribution and the locations named in this paper. The San Francisco Estuary including the Delta has been expanded and shifted right at bottom. Blue rectangles indicate dams.
3. Image plot showing annual distribution of adult passage at RBDD by week. Each rectangle represents the number of fish (log scale, see legend) estimated to have passed the dam during that week. Black lines indicate weeks at which each quartile of the population had passed RBDD. Data are missing for winter-spring starting in 1987 because RBDD gates were open to allow winter Chinook to pass the dam unimpeded. Data source: D. Killam, CDFG, pers. Comm.
4. Results of analysis of thermal mortality data from USFWS (1999). Each data point is the estimated mortality rate of one batch of eggs/alevins from a single female in a single treatment. Winter-run and fall-run results are shown together. Shapes of symbols indicate race, and colors link families of fish. Open symbols indicate treatments in which mortality was either zero or 100%, which we adjusted by calculating the mortality rate as if either 1 fish or all but 1 fish had died. Regression lines were fitted only to data above 13C; however, to calculate mortality for the model the mortality rates below 13C were subtracted from the other mortality rates to remove non-thermal sources of mortality.
5. Reconstructed temperature in the Sacramento River for key locations. Not all locations are shown, mainly those in the upper river and several in the lower river that provided more complete data for the analysis, plus that at Freeport near Sacramento. Blue lines, model estimates of temperature; red lines, temperature data.
6. Estimates of adult abundance in the spawning area. Red Bluff Diversion Dam estimates are given as reported (green triangles, CDFG 2004) and as calculated with error bars (blue lines). Estimates based on carcass surveys used either Petersen or Jolly-Seber methods (CDFG 2004). Also shown is the best-fit line for a constant cohort replacement rate that changed stepwise in 1993 (see Methods).
7. Spawning distributions from aerial redd surveys. Shaded regions indicate the percentage of the redds observed in each reach as displayed in the scale to the right, which also conveys the relative distance of each reach along the winter Chinook spawning grounds. The white line (left axis) gives the number of redds counted. Data source: D. Killam, CDFG, pers. Comm.
8. Survival of eggs and alevins through summer by year calculated by four methods of estimating thermal mortality. Heavy lines used the model shown in Figure 4, and light lines used a threshold of 16C. Blue lines used reconstructed temperature data, and red lines used output from a temperature model.
9. Stock-recruit relationships for winter Chinook. A, Blue symbols for brood years 1967 - 1975, indicated by numbers. Gray symbols are other years: Open squares, 1976 - 1981, open

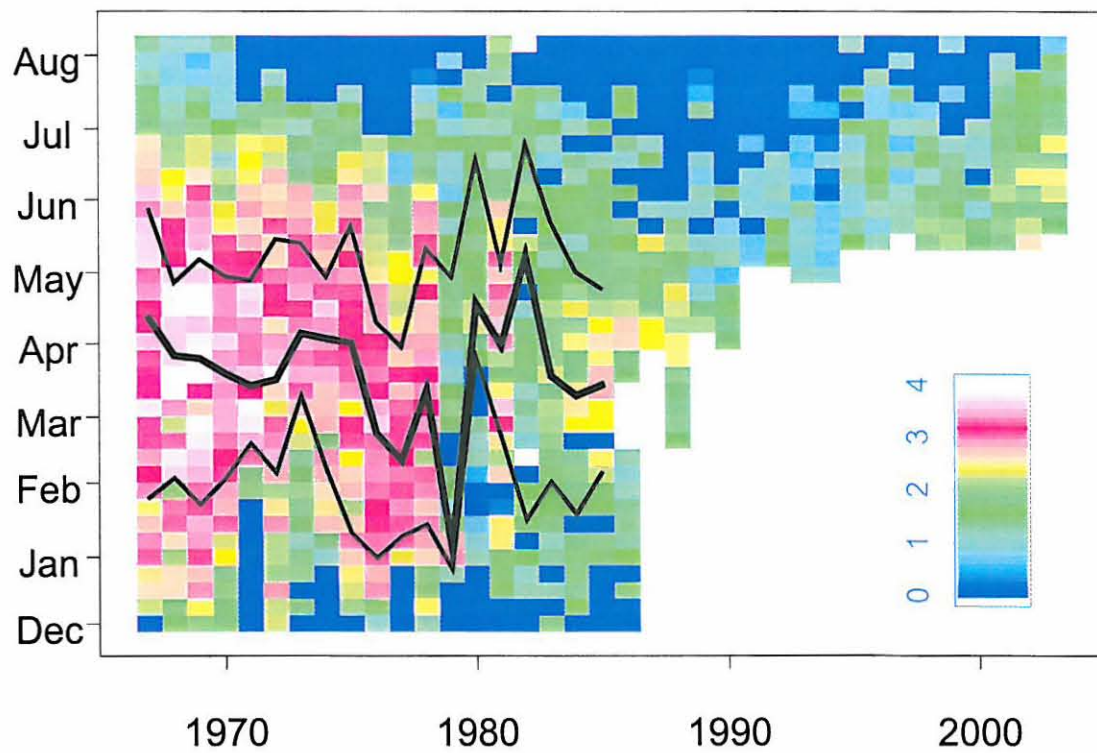
triangles, 1998 - 2002. Green line, rectangular hyperbola with asymptote = $32 \pm 17 \times 10^3$ (95% CL). B, As in A for brood years 1982 - 1997. Asymptote of curve is $1.9 \pm 1.5 \times 10^3$. Note difference in scales. Dashed line is from A. In both A and B the curved lines provided a better fit to the data than a straight line forced through the origin (Akaike Information Criterion).

10. Catches at RBDD and GCID rotary screw traps compared to adult abundance estimates (Figure 2) for 1994 – 2004. RBDD data are in estimated numbers of fish passing the dam. GCID data are in total catch and can be considered an abundance index.
11. Juvenile Chinook passage at six locations. Example for brood year 2004 shows number of fish (log scale with 1 added) per day captured at each of four locations: rotary screw traps sites at RBDD and GCID, beach seine sites on the Sacramento River, trawl sites at Sacramento and Chipps Island, and fish salvage facilities in the south Delta. Data have been aggregated over 1-week time and 5-mm length intervals. Missing data indicate that no samples were taken during that period. Lines indicate the range of lengths over which winter Chinook are assumed to be found. Data sources given in Table 1. Log scales run from 1 to: 630 (RBDD), 16.5 (GCID), 101 (beach seine), 94 (Sacramento trawl), 12 (Salvage), and 58 (Chipps Island trawl).
12. Juvenile winter Chinook emigration past RBDD based on length criteria illustrated in Figure 11. Examples for three years of different hydrology. Each panel gives the catch per day of fish in two size classes, where fish ≤ 60 mm are considered fry and those >60 mm are pre-smolts or smolts. The blue line gives daily mean river flow from Shasta Dam.
13. Juvenile emigration past RBDD. Data for each year consists of total catch in the two size classes for which examples are given in Figure 12. Numbers indicate brood years. The line is a generalized linear model with linear link and variance proportional to the mean. The error bar gives the 95% confidence limits for the intercept, which is significantly different from zero ($p = 0.03$, 7 df).
14. Timing of juvenile winter Chinook passage by three locations, based on length criteria illustrated in Figure 11. Vertical lines give 10th and 90th percentiles, and horizontal bars are medians: Red bars, RBDD; green bars, GCID; gray bars, beach seine sites in the Sacramento River.
15. Migration speed inferred from winter Chinook tagged at LSNFH and recaptured in the river and delta in 1998 - 2003. Results are given for recapture in 4 sampling programs, with 1998 data for the Chipps Island trawl presented separately. Numbers give total fish recaptured for each bar. In 5 of 6 years fish were released between 27 Jan and 1 Feb, but in 1998 fish were released on 9 April and recaptured only at Chipps Island. Differences among years other than 1998 were not significant (ANOVA, $p > 0.05$).
16. Timing of all winter Chinook in-river life stages; adult and juvenile passage based on data in Figures previous figures. Symbols indicate median times of life-history events estimated from data for each year; open symbols indicate emergence times projected from estimated spawning times. The y axis orders events approximately in sequence, with points of passage spread in proportion to distance along the river. Thin lines connect data from individual brood years; note that none of the adult passage data connects because those data do not overlap with the other data (Figure 3). Heavy line connects grand medians of all data. Timing of spawning based on redd surveys and on carcass surveys with an assumed delay of

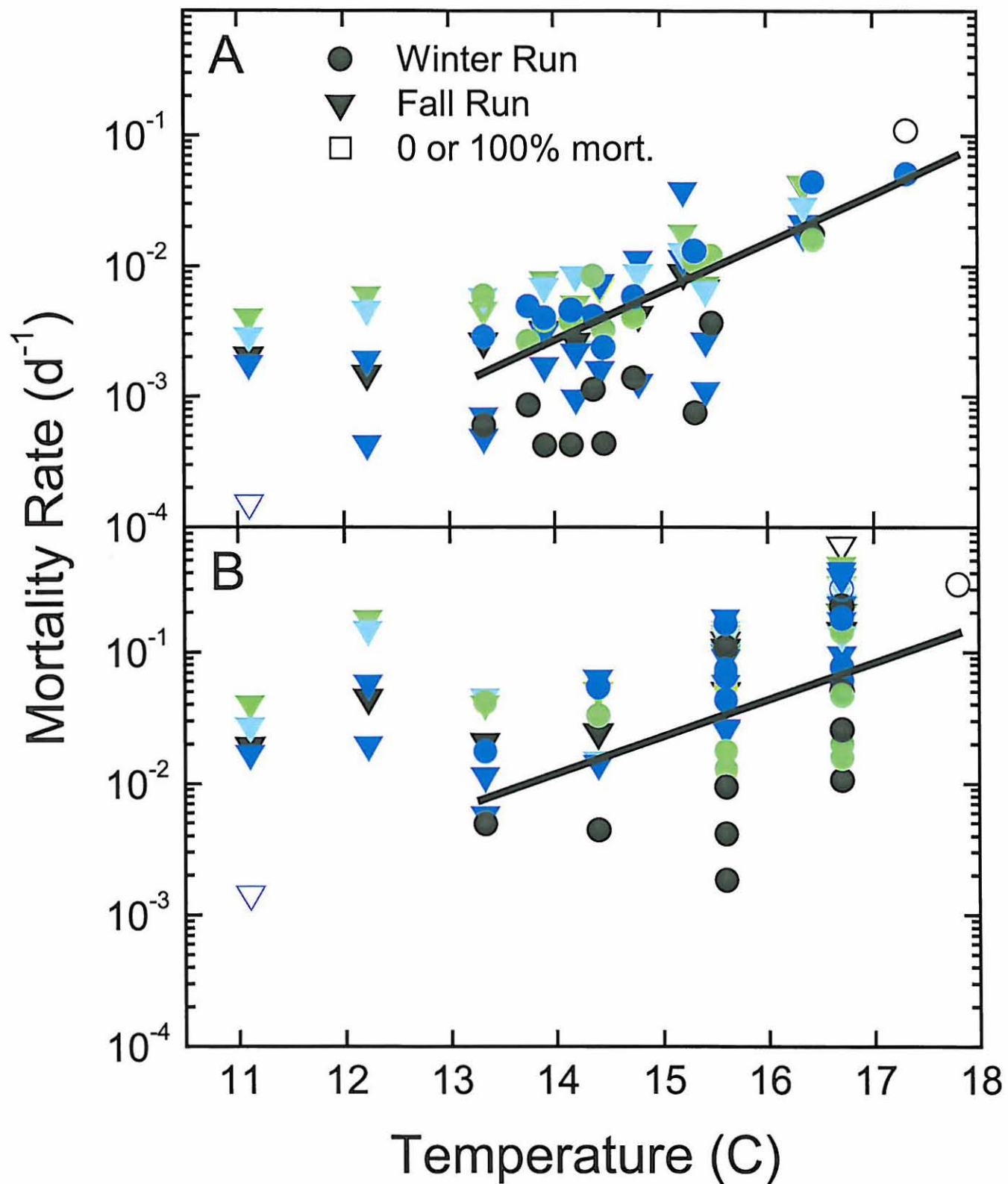
- 2 weeks between spawning and recapture of the carcass (D. Killam, CDFG, pers. Comm.). Timing of emergence was calculated from timing of spawning by projecting forward using river temperature in a Bělehrádek function to estimate daily fractional development to emergence.
17. Timing of juvenile winter Chinook passage by two locations, based on length criteria illustrated in Figure 11. Symbols as in Figure 14: red bars, combined state and federal fish salvage facilities; green bars, Chipps Island.
 18. Data from fish salvage facilities in the south Delta. Light blue symbols represent one or more fish for each day/length combination, with symbol area scaled to the number of fish (1 - 118). Other symbols, genetically determined fish in 10-day by 10-mm blocks. Area of symbols is proportional to the number of fish identified in that block (see key). Open symbols: all fish provisionally identified as winter Chinook (red) or others (blue). Solid symbols, proportion provisionally identified as winter Chinook is shown by color.
 19. Migration speed of marked late-fall Chinook smolts released in the Sacramento River and recaptured at Chipps Island. Error bars give 95% confidence limits of the mean migration speed, and symbol sizes are proportional to the number of fish recaptured (N= 13 to 48).
 20. Ratio of survival indices for late-fall Chinook released at Georgiana Slough to those released at Ryde or Isleton, downstream from Georgiana Slough on the Sacramento River, plotted against export flow at state and federal pumps in the south Delta. Survival ratios provided by P. Brandes (USFWS). A, survival indices based on recovery in the Chipps Island trawl; B, survival indices based on recovery in the ocean fishery as of May 2005. Red symbols give the export flow on the 20th day after release, and horizontal lines give the range of export flows during the 20 days after release. See Table 8 for regression parameters.
 21. Estimated mortality of winter Chinook in the ocean fishery. Lines give (top to bottom) the harvest fraction [catch / (catch + escapement)], the fishing mortality estimated from harvest fraction assuming 20% annual natural mortality, and the fishing mortality for winter Chinook. Symbols show the total mortality due to fishing on winter Chinook estimated by mark-recapture studies for 6 years. .
 22. Cohort replacement rate from the data (line with symbols) and the model (plain line).
 23. Slopes and 90% confidence limits for regressions of residual cohort replacement rate vs. standardized environmental variables. Some variables have had their signs reversed so that a positive slope would indicate that environmental variable had an effect expected by its mode of influence. For example, high temperature would be expected to reduce survival making the residual negative, so with a reversed sign a significant temperature effect would have a positive slope.



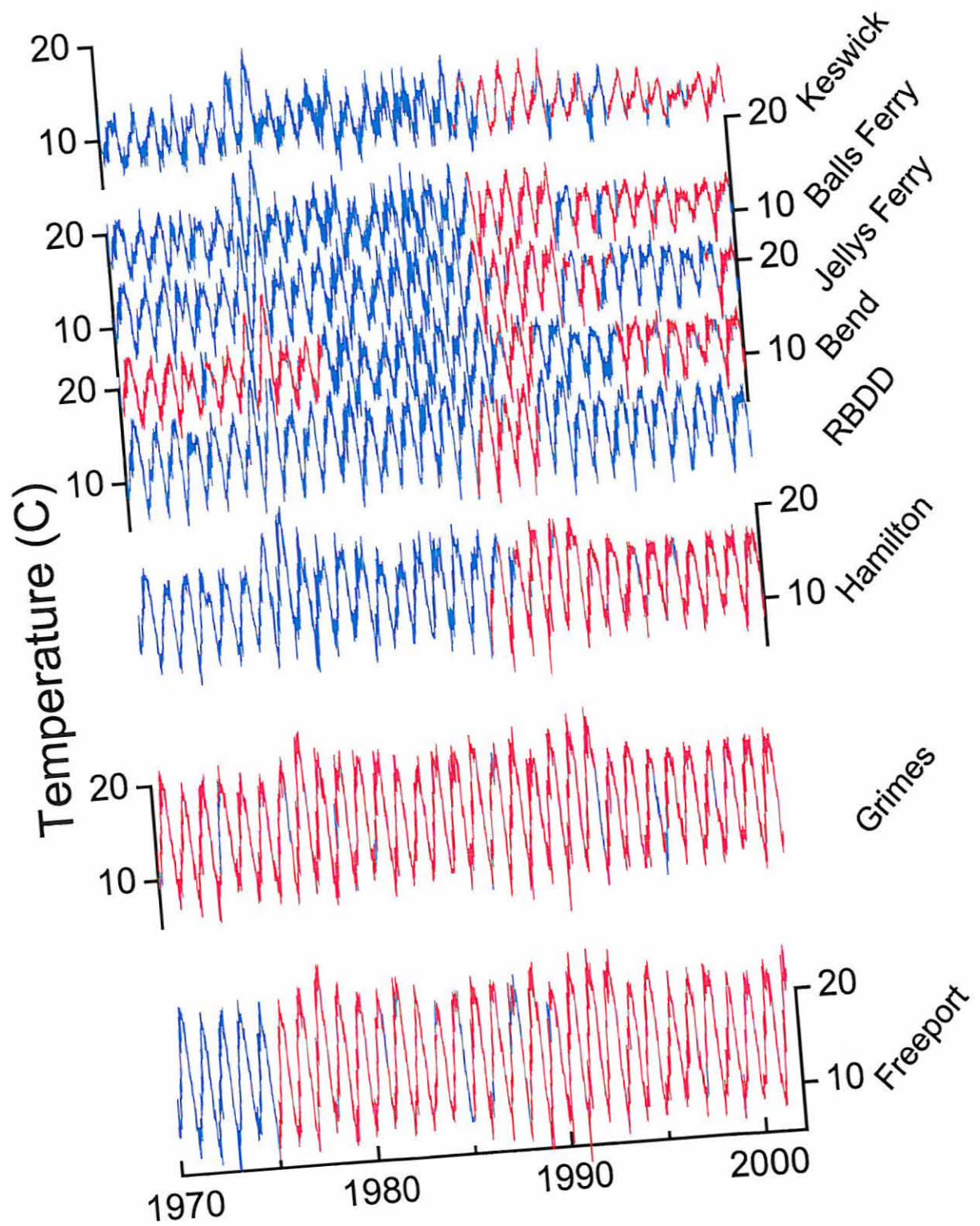




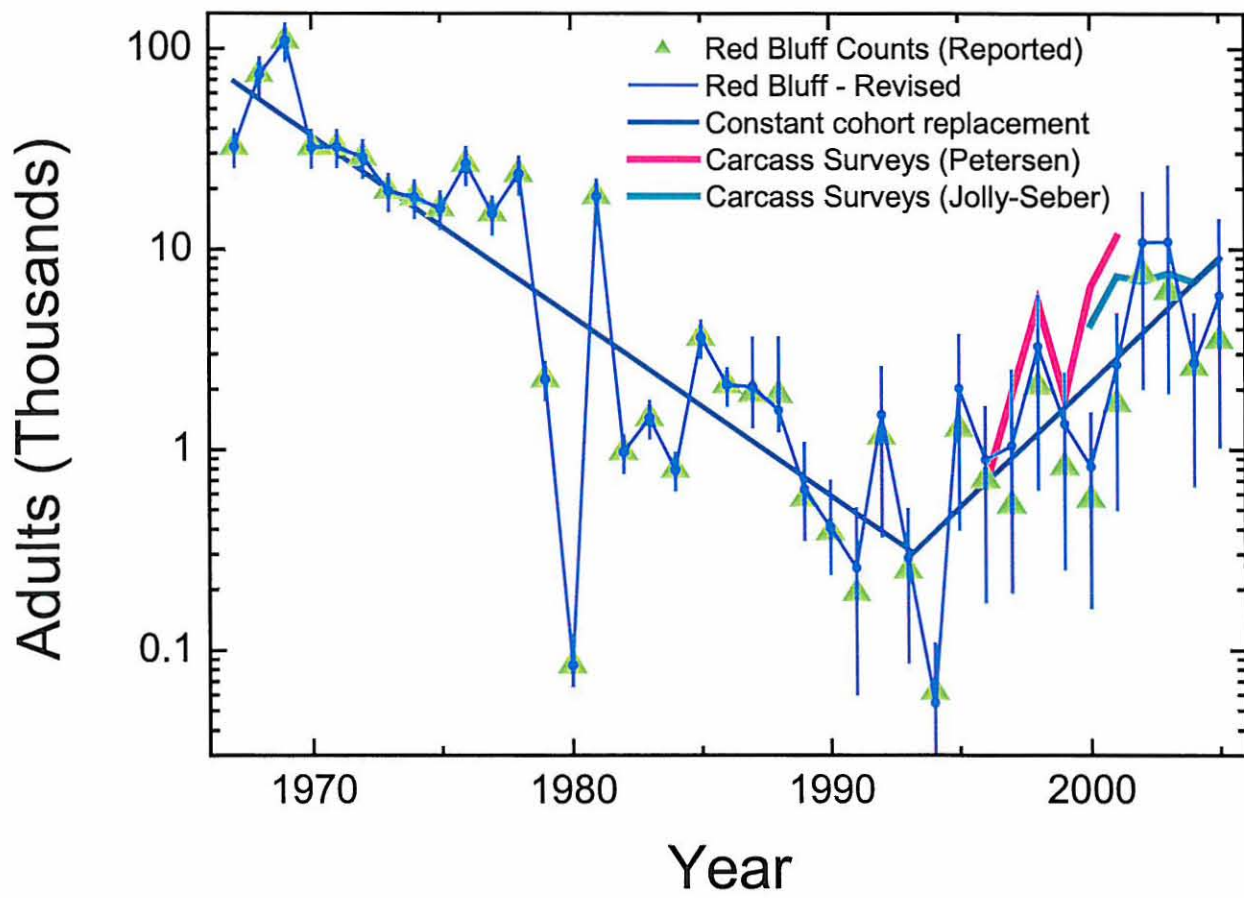
Kimmerer and Brown Figure 3



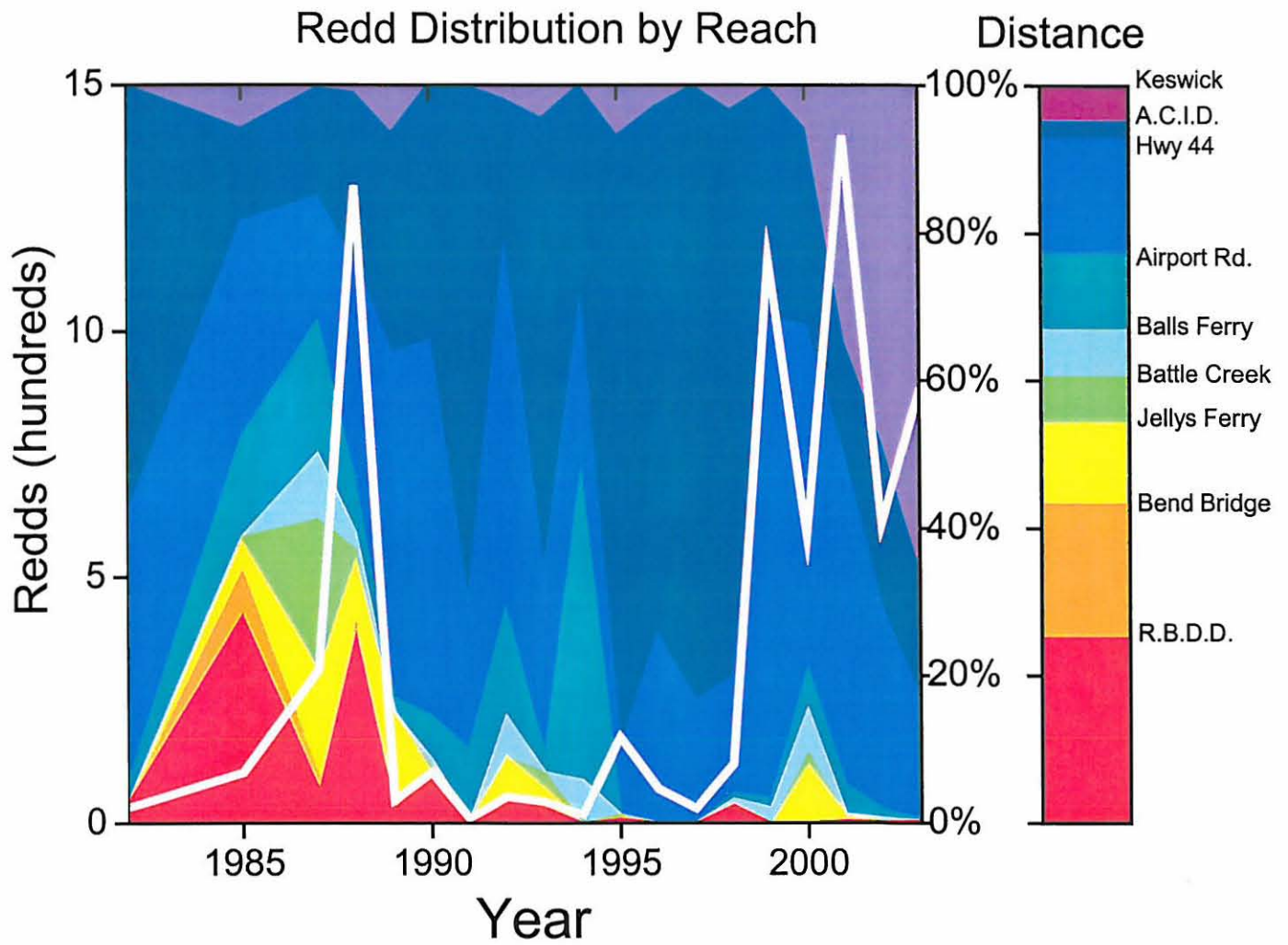
Kimmerer and Brown Figure 4



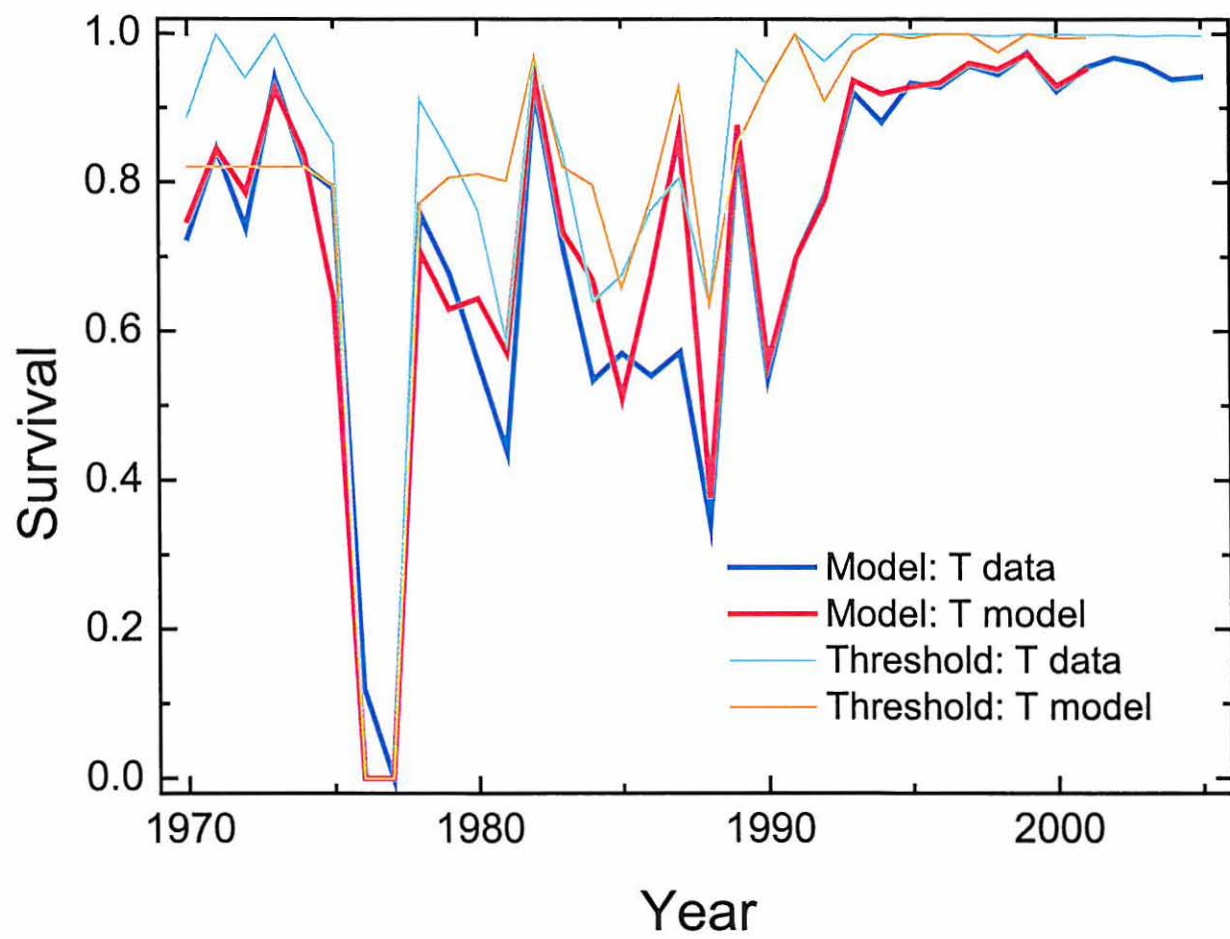
Kimmerer and Brown Figure 5



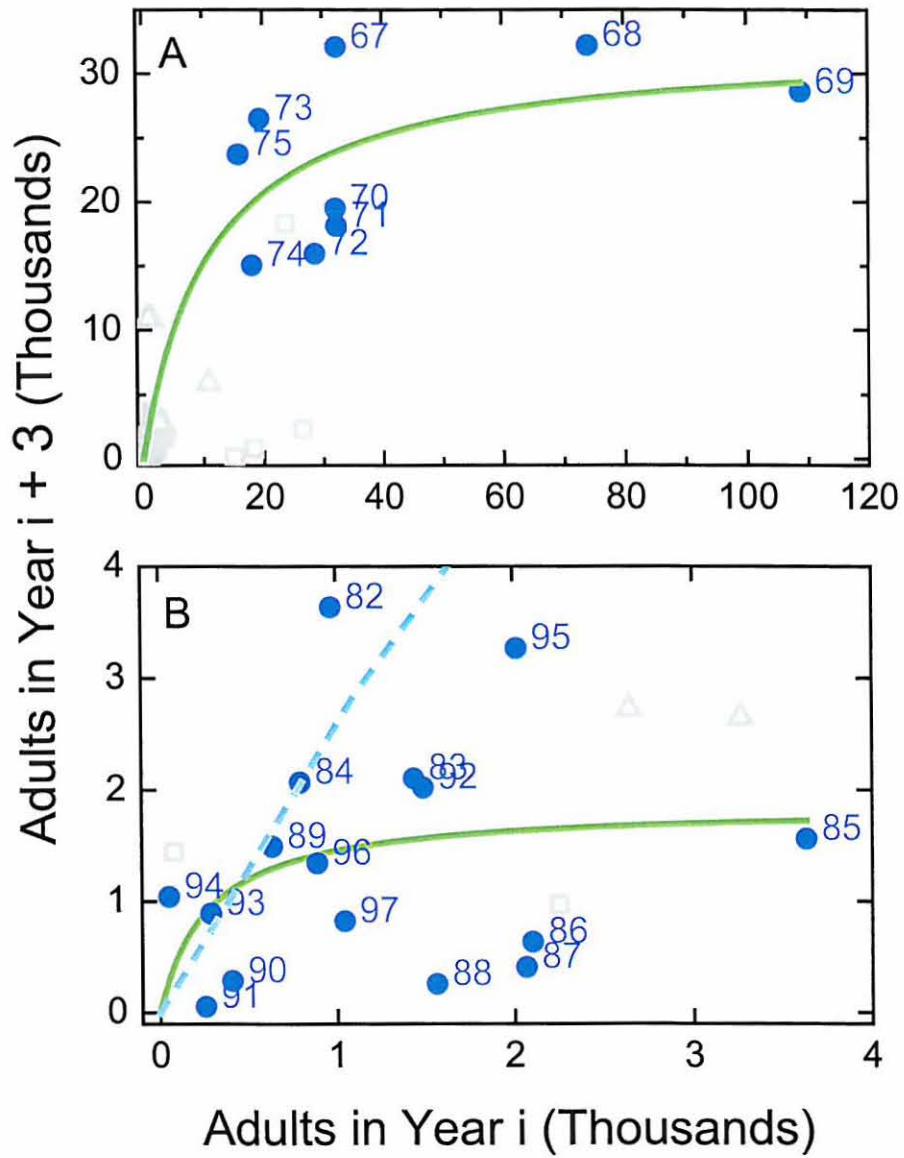
Kimmerer and Brown Figure 6



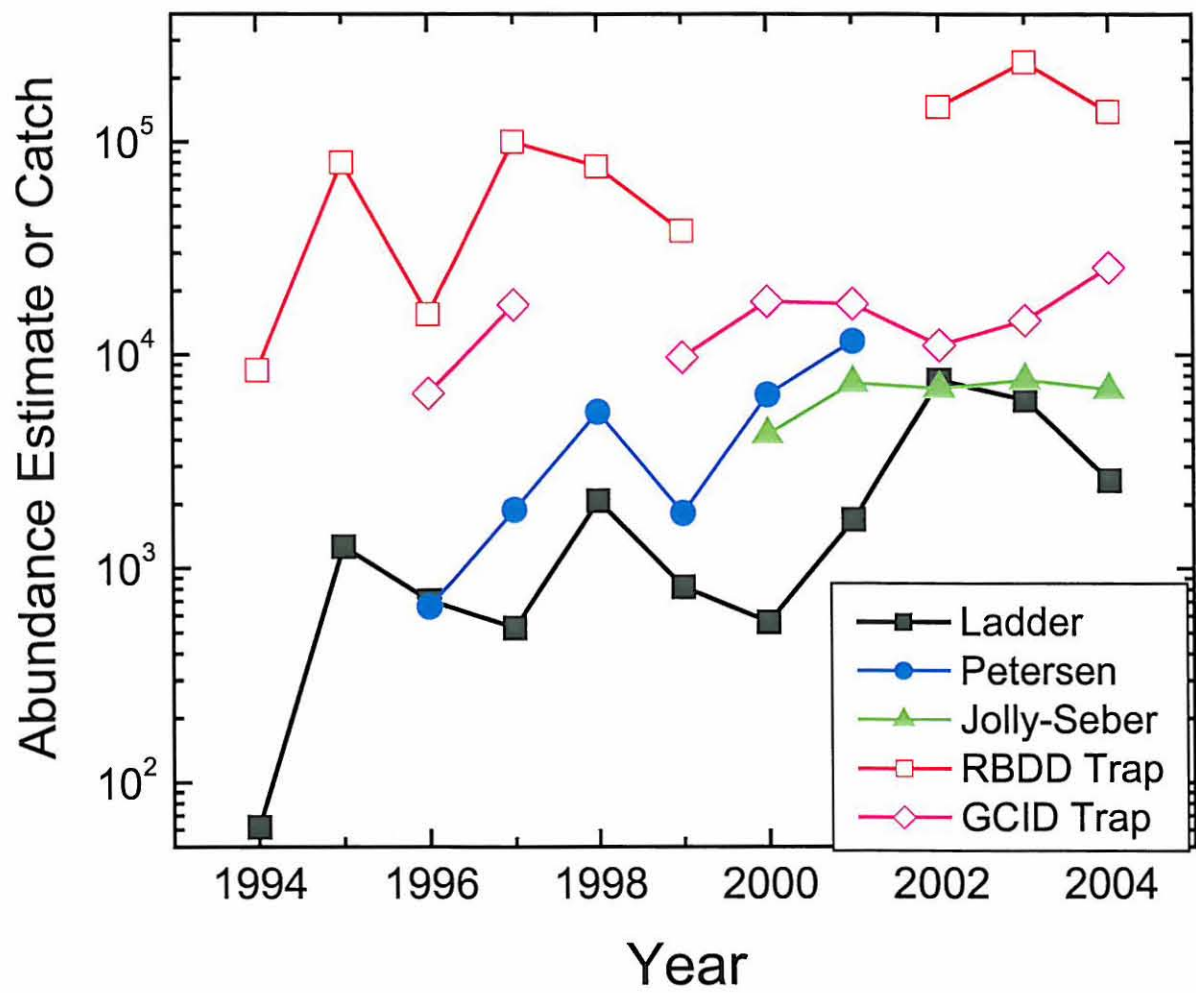
Kimmerer and Brown Figure 7



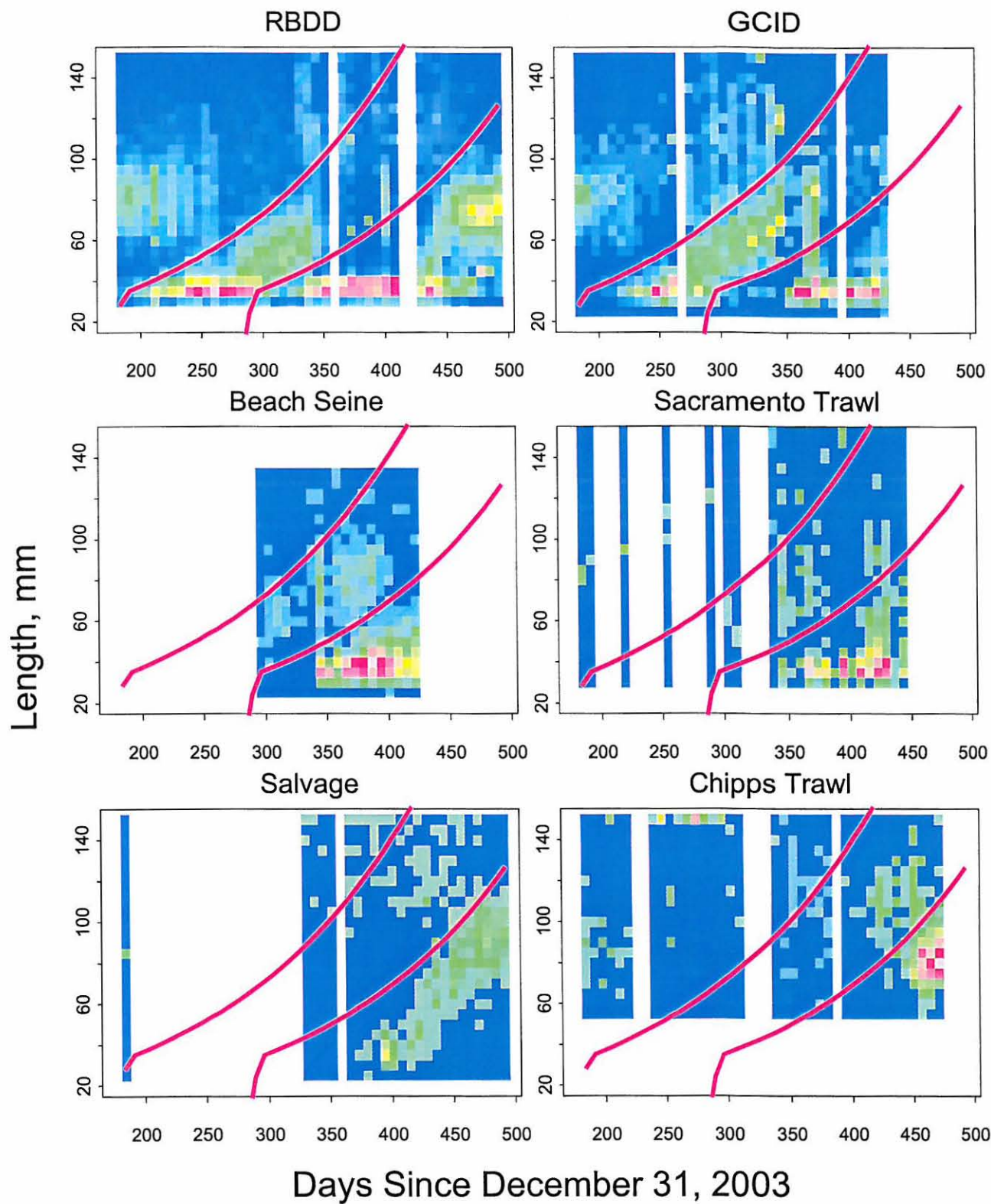
Kimmerer and Brown Figure 8



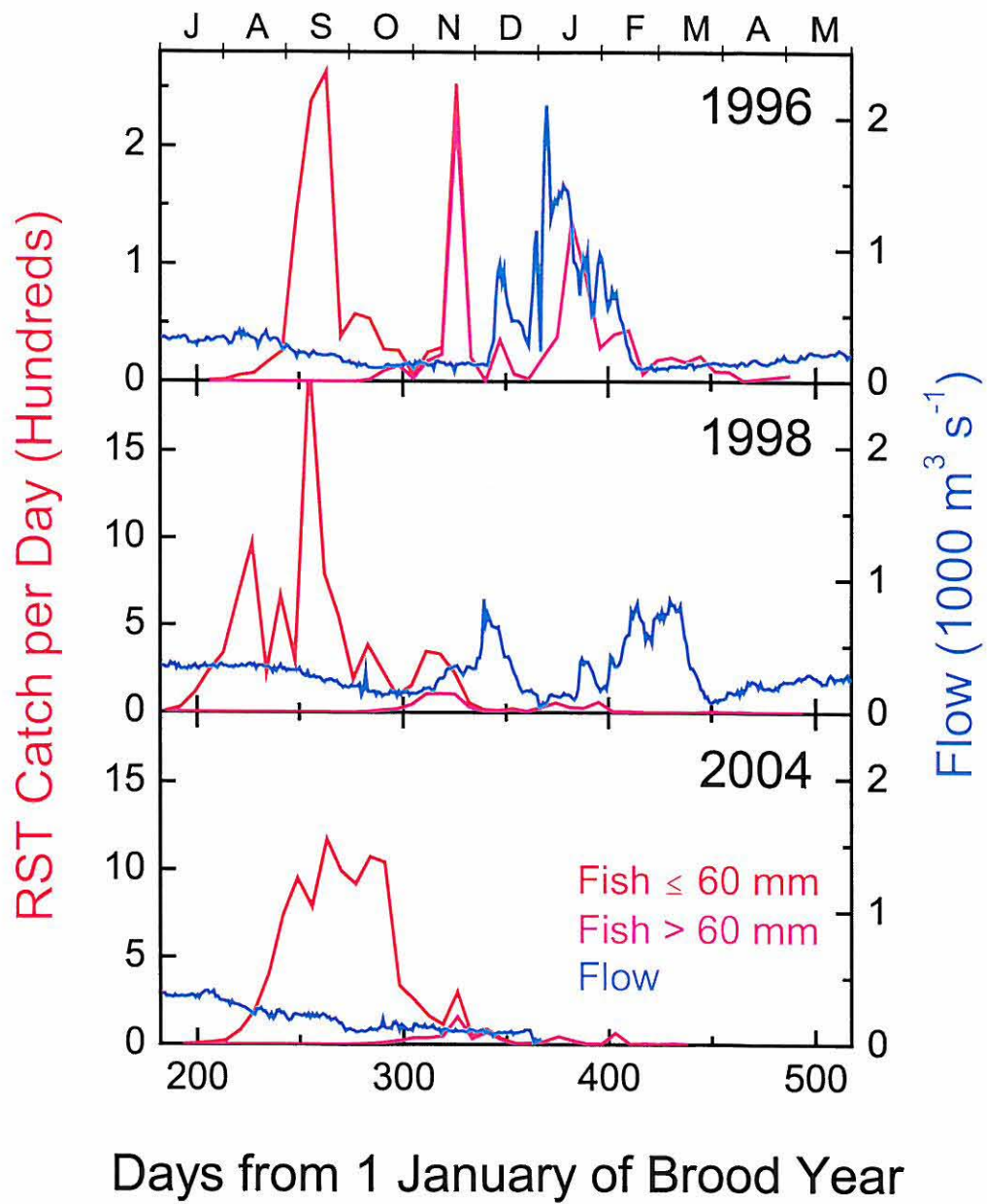
Kimmerer and Brown Figure 9



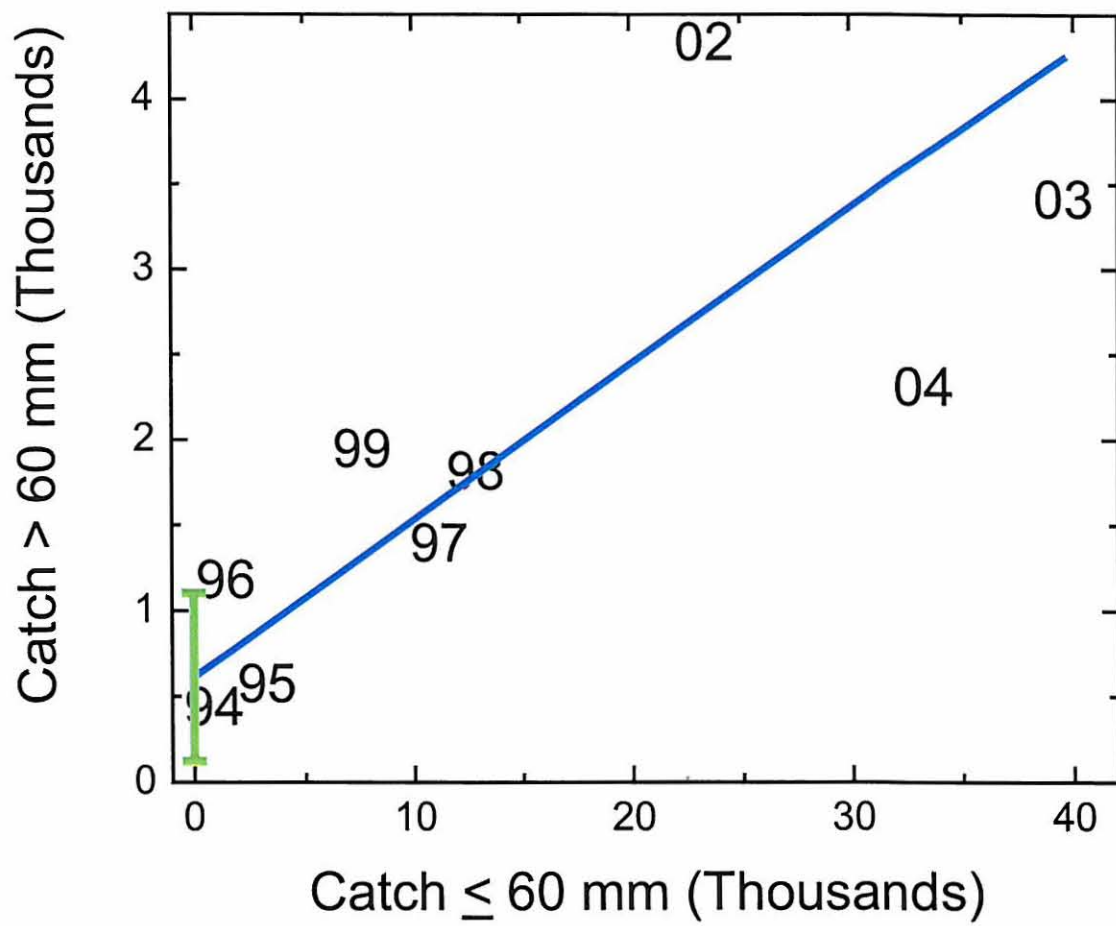
Kimmerer and Brown Figure 10



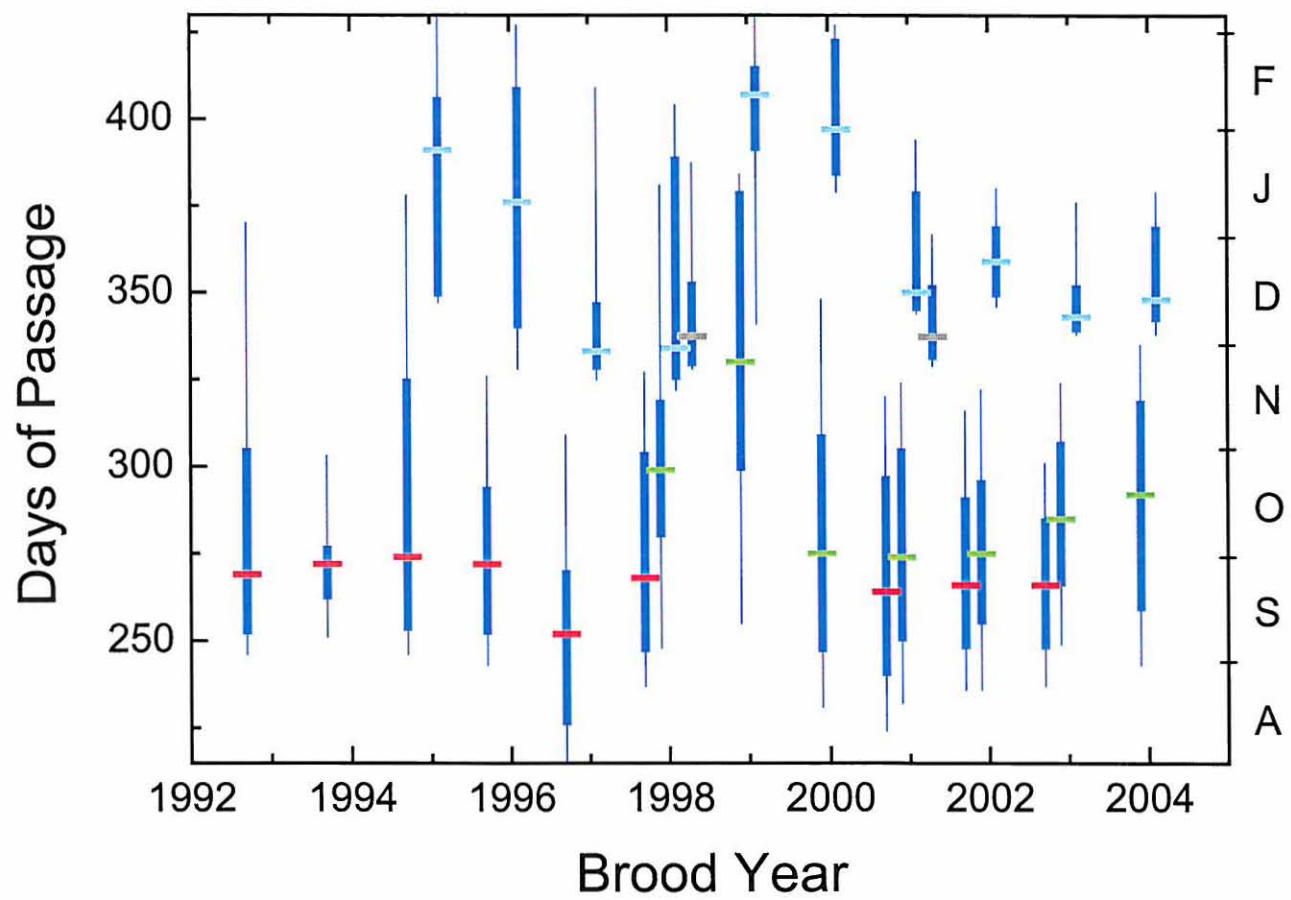
Kimmerer and Brown Figure 11



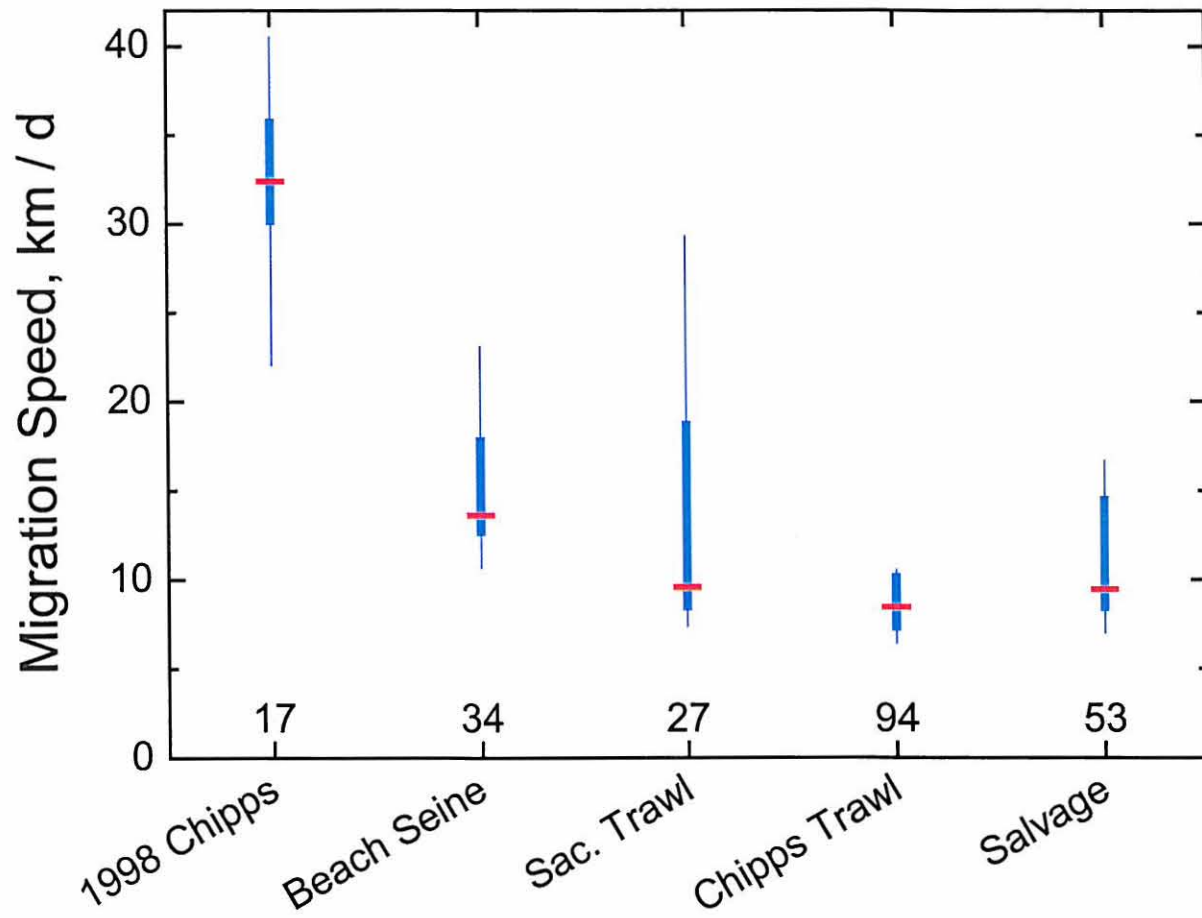
Kimmerer and Brown Figure 12



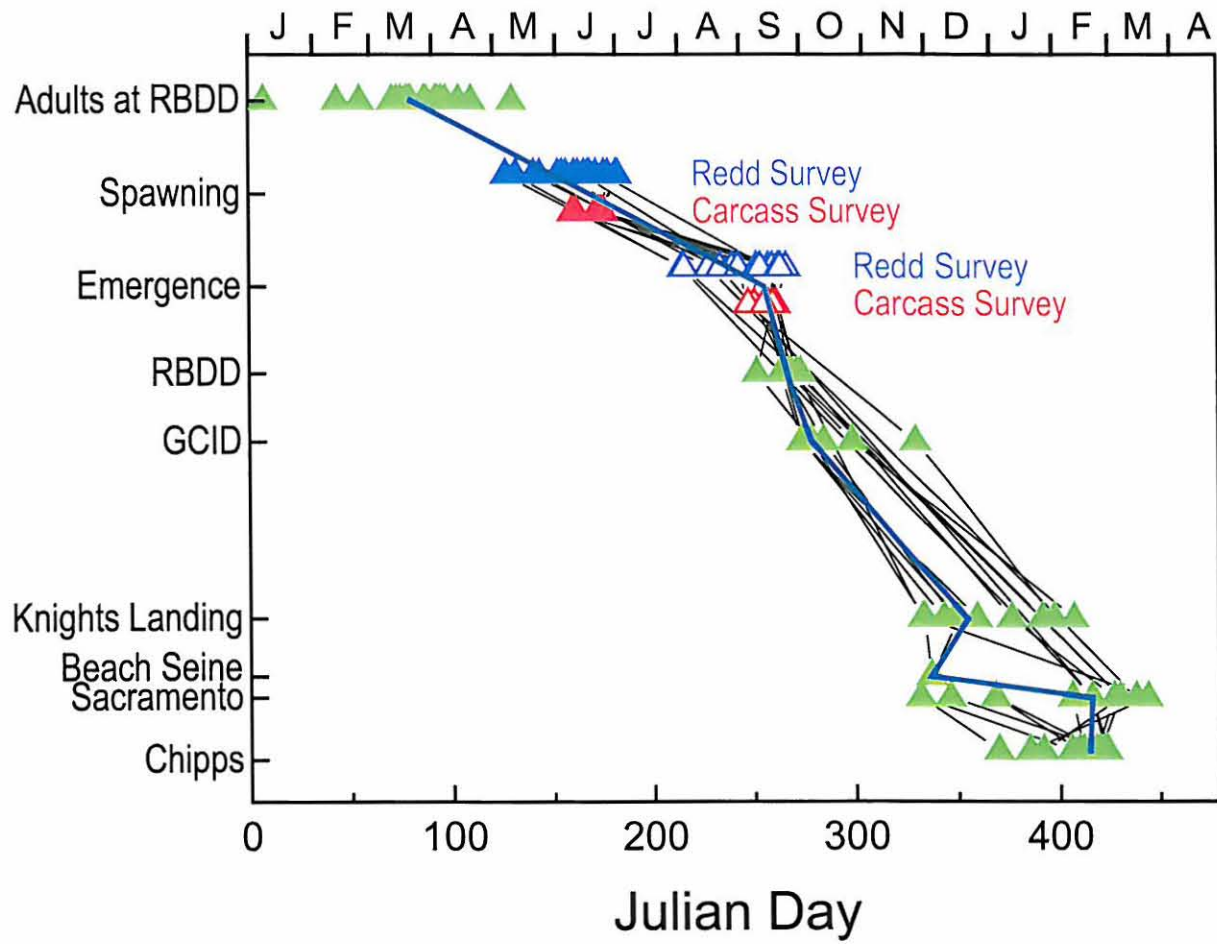
Kimmerer and Brown Figure 13



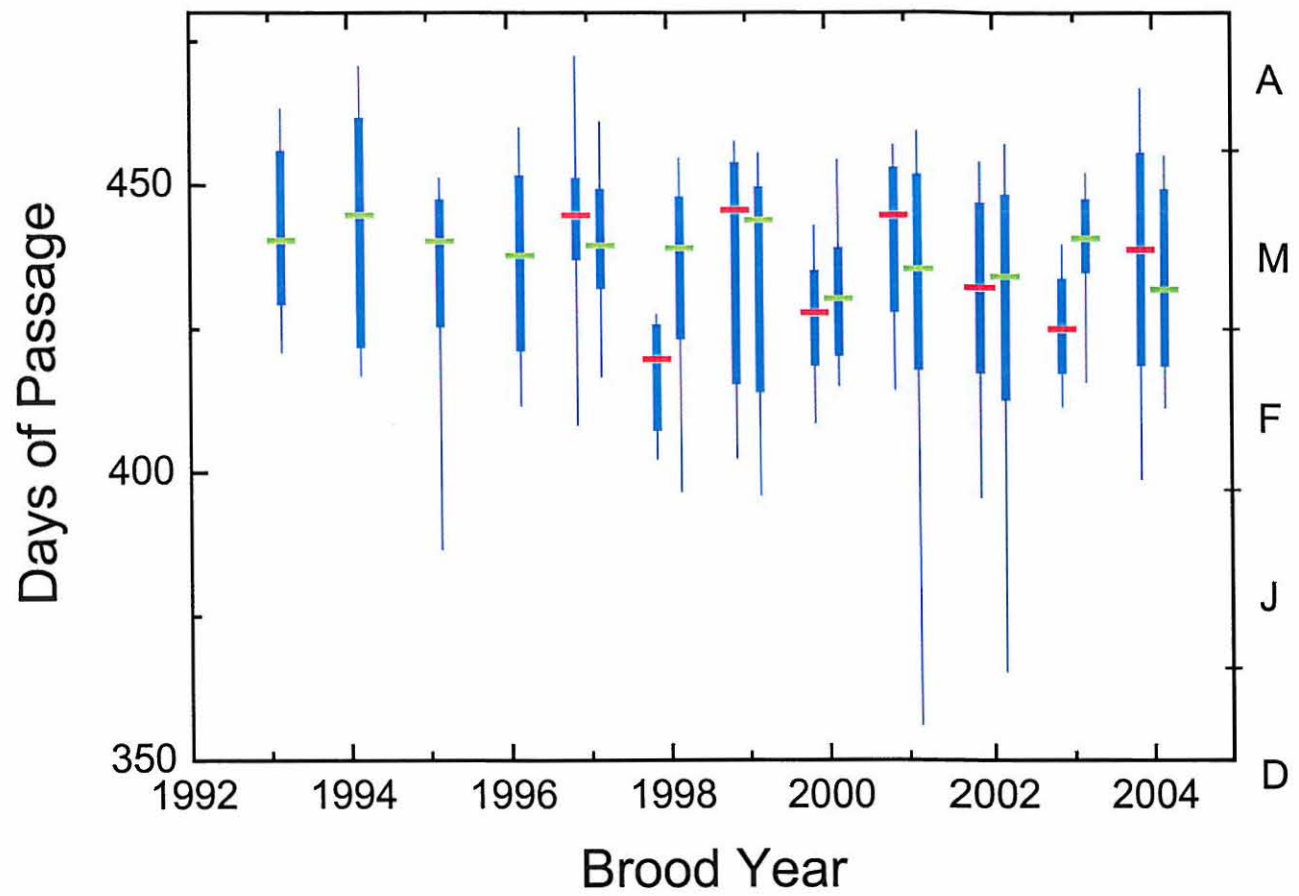
Kimmerer and Brown Figure 14



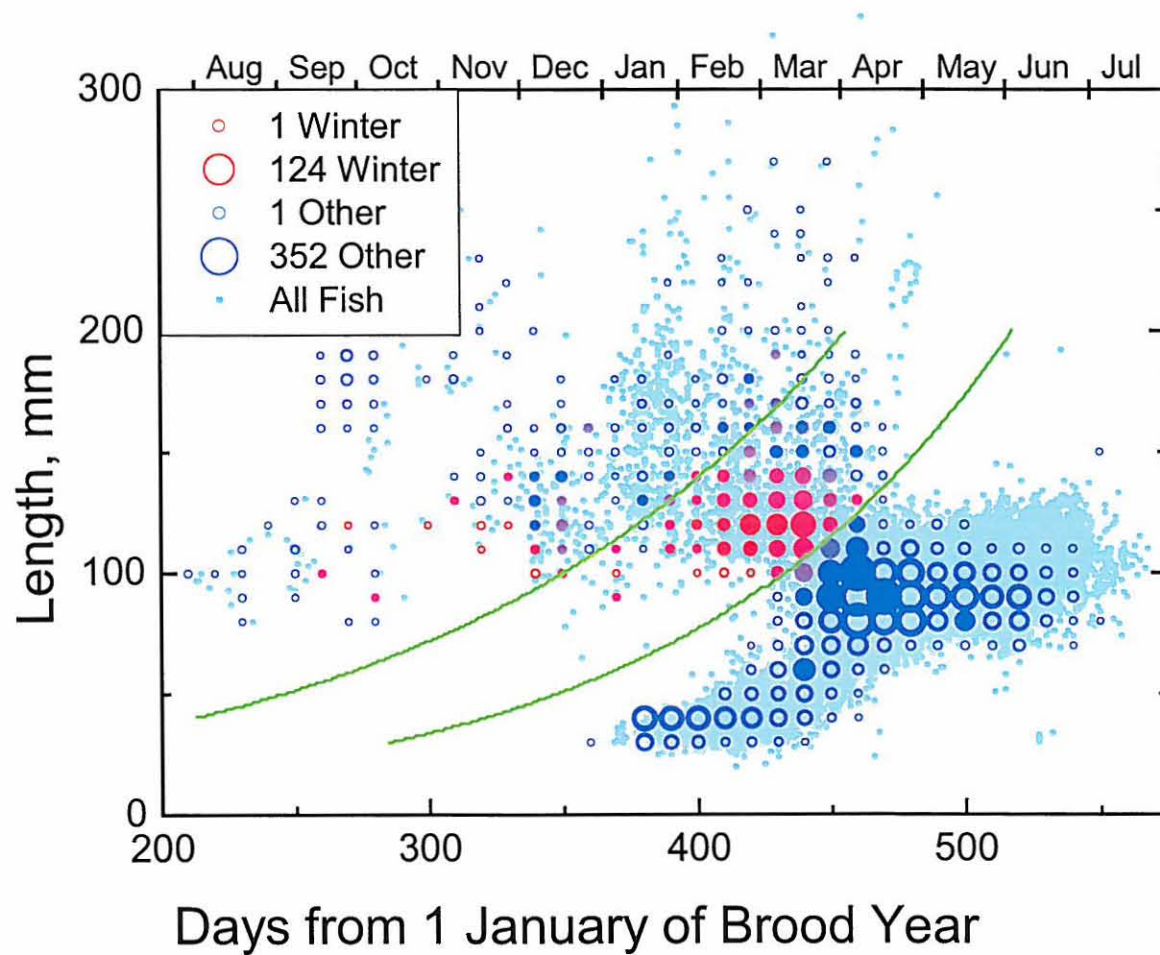
Kimmerer and Brown Figure 15



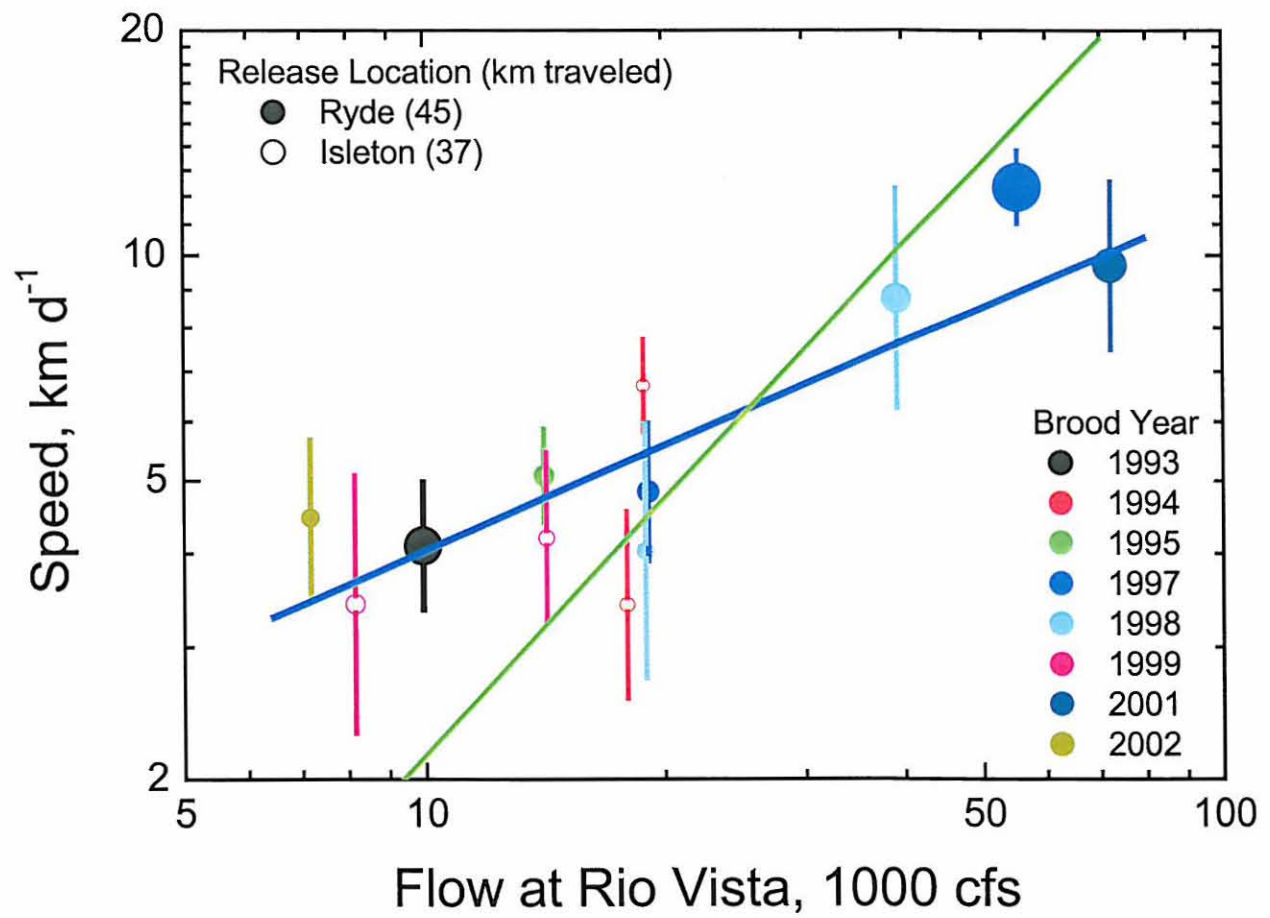
Kimmerer and Brown Figure 16



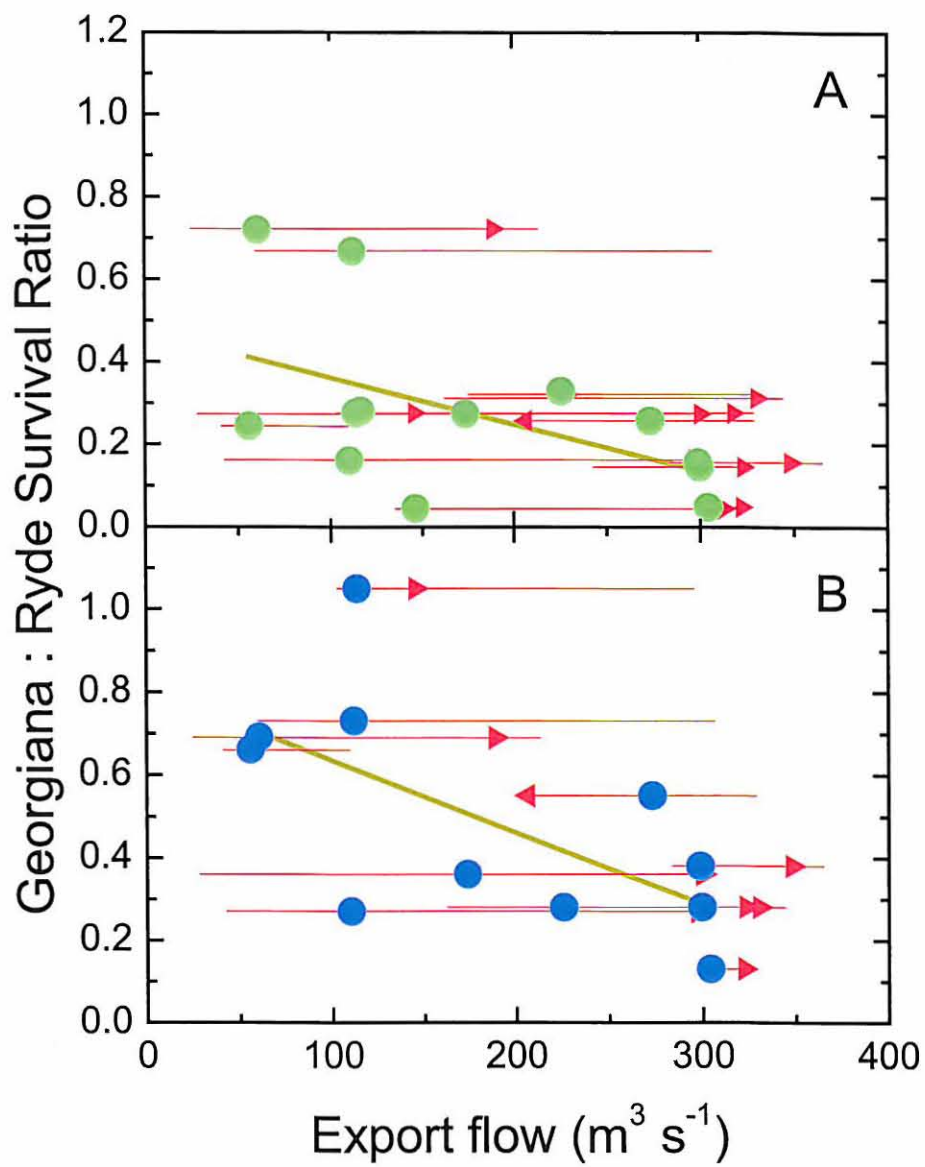
Kimmerer and Brown Figure 17



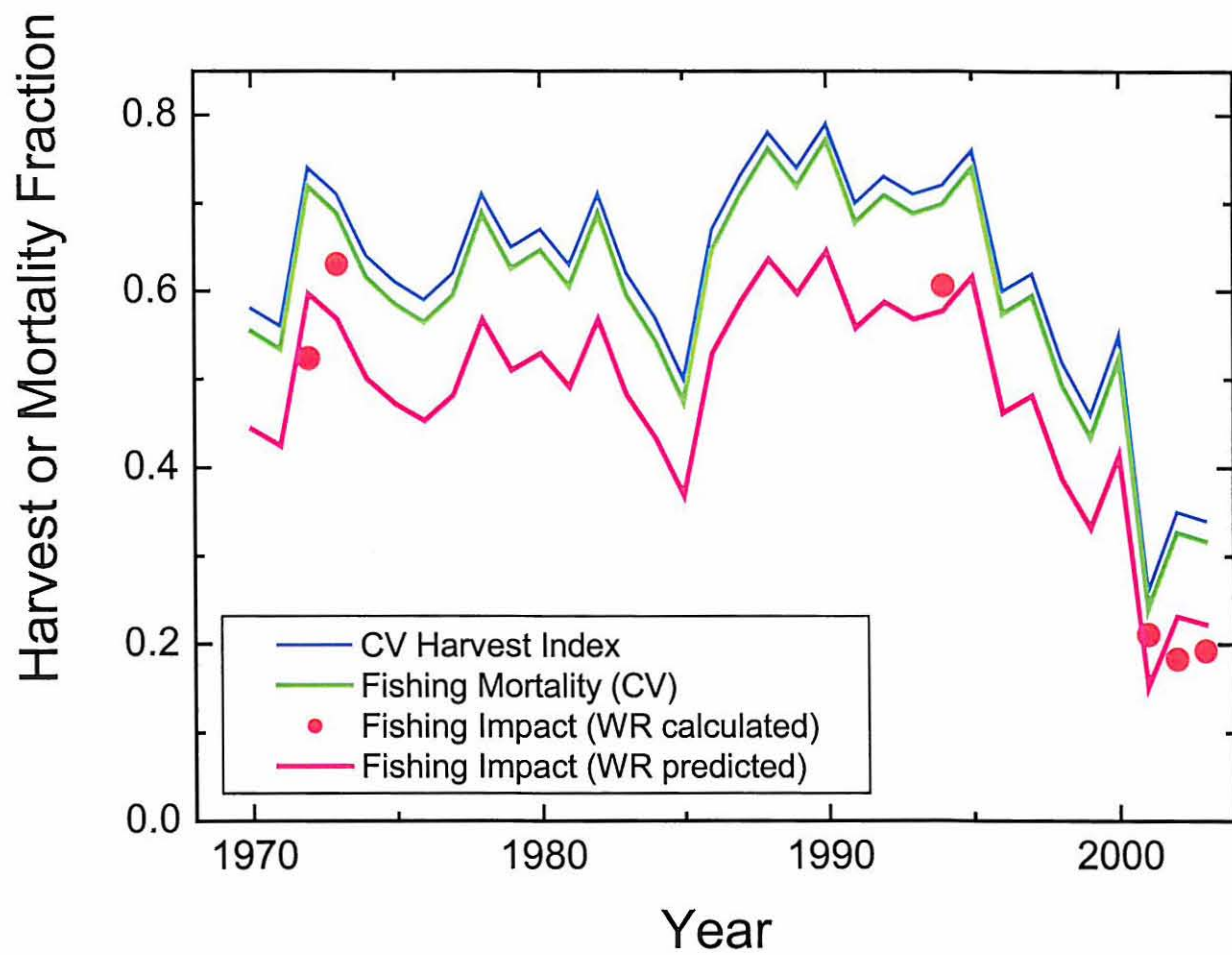
Kimmerer and Brown Figure 18



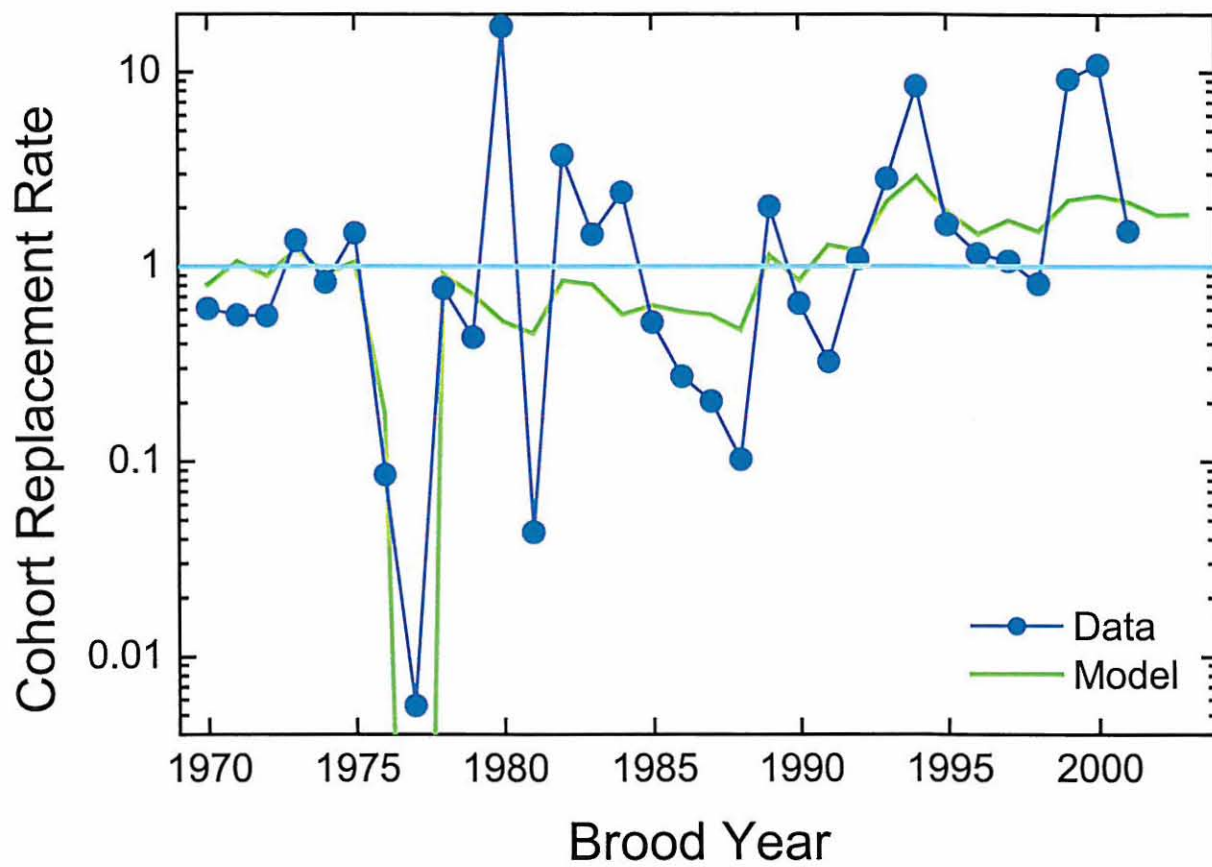
Kimmerer and Brown Figure 19



Kimmerer and Brown Figure 20



Kimmerer and Brown Figure 21



Kimmerer and Brown Figure 22

Standardized Coefficient

